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# Co-occurrence history increases ecosystem stability and resilience in experimental plant communities

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**Running head: Co-occurrence history boosts stability**

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## Abstract

Understanding factors that maintain ecosystem stability is critical in the face of environmental change. Experiments simulating species loss from grassland have shown that losing biodiversity decreases ecosystem stability. However, as the originally sown experimental communities with reduced biodiversity develop, plant evolutionary processes or the assembly of interacting soil organisms may allow ecosystems to increase stability over time. We explored such effects in a long-term grassland biodiversity experiment with plant communities with either a history of co-occurrence (selected communities) or no such history (naïve communities) over a four-year period in which a major flood disturbance occurred.

Comparing communities of identical species composition, we found that selected communities had temporally more stable biomass than naïve communities, especially at low species richness. Furthermore, selected communities showed greater biomass recovery after flooding, resulting in more stable post-flood productivity. In contrast to a previous study, the positive diversity–stability relationship was maintained after the flooding. Our results were consistent across three soil treatments simulating the presence or absence of co-selected microbial communities. We suggest that prolonged exposure of plant populations to a particular community context and abiotic site conditions can increase ecosystem temporal stability and resilience due to short-term evolution. A history of co-occurrence can in part compensate for species loss, as can high plant diversity in part compensate for the missing opportunity of such adaptive adjustments.



*Key words: asynchrony; co-occurrence history; disturbance; grassland biodiversity; recovery; resistance; flood; selection; diversity – stability relationship*

## INTRODUCTION

Biodiversity experiments simulating the loss of plant species from grassland communities have shown that less diverse communities have reduced mean (Balvanera et al. 2006, Cardinale et al. 2012) and increased temporal variation in aboveground biomass (Tilman et al. 1998, 2006, Hector et al. 2010). However, it is not clear whether these communities may regain functioning and stability over time while still being at low diversity. The few biodiversity experiments that lasted more than 10 years showed that functioning tended to decrease in low-diversity communities and to increase in high-diversity communities, leading to an increased slope of the biodiversity–biomass production relationship over time (Reich et al. 2012, Meyer et al. 2016, Guerrero-Ramírez et al. 2017). In one of these experiments, the Jena Experiment in Germany (Weisser et al. 2017), it was shown that divergent evolutionary changes of plant species in monocultures vs. mixtures during the first 8 years contributed to this strengthening of the biodiversity–functioning relationship (Zuppinger-Dingley et al. 2014, van Moorsel et al. 2018, 2019). Feedbacks between plants and soil organisms, however, had less explanatory power (van Moorsel et al. 2018, Schmid et al. 2019, Hahl et al. 2020).

Ecosystem resistance, recovery, and resilience that underlie stability may depend on plant diversity (Pfisterer and Schmid 2002, Isbell et al. 2015, Fischer et al. 2016). The mechanisms by which diversity stabilizes ecosystem biomass production are based on differences among genotypes or species in their responses to the abiotic or biotic environment (Schmid 1994, Tilman et al. 1998, Hector et al. 2010). This response diversity (Elmqvist et al. 2003, Isbell et al. 2011) could increase over time. Evolution in communities may lead to divergence in trait expression between species via selection for genetically fixed divergent phenotypes or via selection for genotypes

with increased trait plasticity (Zuppinger-Dingley et al. 2014, Meilhac et al. 2020). By extension, similar processes may also occur between genotypes within monocultures (Henn et al. 2018, van Moorsel et al. 2018). Such a greater trait diversity between species in mixtures (or within species in monocultures) may result in greater response diversity or temporal niche occupation and thus greater stability (de la Riva et al. 2017, Hallett et al. 2017). These processes may even be more important in low-diversity communities because of closer interactions between the few remaining species and of the refilling of community niche space (Salles et al. 2009). In contrast, in more diverse communities, such opportunities for evolutionary adjustments may be more limited.

Asynchrony among species performances in terms of biomass production can allow diverse communities to resist disturbance or recover to maintain performance, often referred to as insurance or portfolio effect (Yachi and Loreau 1999, Hector et al. 2010, Thibaut and Connolly 2013, de Mazancourt et al. 2013). The development of stability over time in long-term biodiversity experiments has not been analyzed so far, but in the Jena Experiment (Weigelt et al. 2010, Weisser et al. 2017) combined intra- and inter-annual biomass variation in experimental communities decreased over time for the first 8 years (i.e. ecosystem stability, measured as the inverse of the coefficient of variation of plant biomass, increased over time; Appendix S1: Fig. S1A). During this time, climatic stability did not increase but the stability of interannual precipitation did increase (Appendix S1: Fig. S1B, C, D). This correlation between precipitation and biomass stability demonstrates a fundamental problem of interpretation in studies that confound (community) age and physical time. Therefore, we designed an experiment that separated the two.

We hypothesize that the increase in biomass stability over time in the Jena Experiment can at least in part be attributed to community age. As communities develop following sowing, species abundance distributions and gene frequencies change, and such adjustments between and within species may increase stability (Strauss et al. 2006, Aubree et al. 2020). We addressed our overall hypothesis by comparing such "old" communities with "new" communities of the same species composition at the same time and under the same environmental conditions. We use "co-occurrence history" when we refer to plant species with a history of growing in the company of one another over a certain period of time, potentially developing stronger interactions or associations with both the plant and soil community partners over time.

A prolonged period of co-occurrence can increase "stabilizing differences" between phylogenetically distinct annual plant species in comparison with similar pairs of species without co-occurrence history over a long time span (Germain et al. 2016) and, in theory, co-adaptation can modify biodiversity–productivity and biodiversity–stability relationships also over shorter time spans (Aubree et al. 2020). Here we ask if prolonged co-occurrence within a local community can result in changed species interactions and reduced competition in the short term, such as during the course of a biodiversity experiment, and not only for annual but also for perennial species. In addition, we applied different soil treatments to assess the potential contribution of soil organisms that over time associate with plant communities and may (de)stabilize plant communities by changing nutrient provision and the plant's health (Eisenhauer et al. 2011, 2012). Our experimental communities ranged in richness from one, two and four to eight plant species. We refer to "old" communities as "*selected* communities" since they were assembled with offspring

from individuals that had co-occurred in the same plots of the Jena Experiment over 8 years from 2002–2010. We refer to "new" communities as "*naïve* communities" because they were assembled with offspring from seeds that were obtained from the original seed supplier for the Jena Experiment. We grew these communities from 2012–2015 within cleared space in the original plots of the Jena Experiment.

We previously found that selected communities were more productive than naïve communities in the same experiment at the 2- and 4-species richness levels but not at the 8-species richness level. We thus firstly hypothesized (1) that selected communities have more stable biomass than naïve communities and that differences in stability between selected and naïve communities are most pronounced at low to intermediate diversity (hypothesis 1). Secondly, we hypothesized that stability is further increased when plants grow with their native soil organisms (hypothesis 2).

A flood in summer 2013 (Blöschl et al. 2013) allowed us to analyze the resistance, recovery, and resilience (Ruijven and Berendse 2010, Lloret et al. 2011, Hillebrand et al. 2018) of our communities in response to this disturbance. Together, resistance and recovery determine ecosystem resilience as we define it here, namely how ecosystem biomass production differs between pre- and post-disturbance states (Lloret et al. 2011). We hypothesized that co-occurrence history should also increase stability towards perturbation, thus that selected communities show greater resistance, recovery, and resilience in response to the flood event (hypothesis 3).

## METHODS

### Field site

This study was conducted at the Jena Experiment field site (Jena, Thuringia, Germany, 51 ˚N, 11 ˚E, 135 m a.s.l.) from 2011–2015. The Jena Experiment is a long-

158 term biodiversity field experiment located on the banks of the Saale River. In 78
159 experimental field plots of different diversity levels, 60 mostly perennial species
160 typically forming species-rich grassland ecosystems under low-intensity management
161 are grown in a number of species combinations since 2002 (Roscher et al. 2004).
162
163 **Co-occurrence (selection) history**
164 This study included eleven monocultures, twelve 2-species mixtures, twelve 4-species
165 mixtures and twelve 8-species mixtures for a total of 47 species compositions
166 assembled from a pool of 49 species in the large plots of the Jena Experiment
167 (Roscher et al. 2004). This subset of large plots excluded 16- and 60-species mixtures
168 as well as monocultures and mixtures with very poor growth of some species to obtain
169 nearly equal replication of communities at each diversity level (one initially chosen
170 monoculture could not be used because it contained individuals of a different species
171 from the one originally planted, van Moorsel et al. 2018). The 49 species were mostly
172 outcrossing perennials and represented the functional groups grasses (including
173 graminoids of families other than Poaceae; 16 species), legumes (Fabaceae; 12
174 species) and herbs (21 species, Appendix S1: Table S5).
175 We used two co-occurrence-history treatments: communities assembled with
176 offspring of plants that had grown together for 8 years in the 47 large plots of the Jena
177 Experiment ("selected" communities, Appendix S1: Table S5) and communities
178 assembled with plants without a common history of co-occurrence in the Jena
179 Experiment ("naïve" communities). The naïve communities were naïve in the way
180 that they had not experienced selection in communities in the Jena Experiment but
181 have been exposed to selection in their original field sites and the monoculture
182 gardens of the seed supplier.

183 In total, there were 219 selected populations from different diversity levels in
184 the Jena Experiment for the 49 species. The plants of naïve communities were grown
185 from seeds obtained in 2010 from the same commercial supplier (Rieger Hofmann
186 GmbH, in Blaufelden-Raboldshausen, Germany) who provided the seeds used for the
187 establishment of the Jena Experiment in 2002. The supplied seeds for both the
188 original seed lots in 2002 and the new seed lots in 2010 originated from various field
189 sites in Germany and had been cultivated by reseeding every year for up to five years
190 in monoculture. We could not use seeds from the original lots for the naïve
191 communities because there was not enough seed material left, some species had low
192 germination rates and we were concerned that the long storage might have affected
193 seed quality. The new seed lots from 2010 likely contained other genotypes than the
194 original seeds lots from 2002, but we focused on the species- and community-level
195 replication to test our evolutionary hypotheses. We assumed a random variation for
196 potential biases between seed lots from 2002 and 2010 for each of the 49 species and
197 each of the 141 assembled communities (47 species compositions x 3 soil treatments).
198 These biases could have inflated the error terms used in the hypothesis tests of the
199 mixed models described below and thus reduced observed effect sizes for the term co-
200 occurrence history.
201 To reduce potential maternal carry-over effects from the field, seeds of
202 selected communities were produced in an experimental garden in Zurich,
203 Switzerland, from cuttings that had been made in the Jena Experiment in 2010.
204 Cuttings from multiple individuals per species were planted in Zürich in the original
205 species combination in plots fenced with plastic netting to minimize cross-pollination
206 between the plots and surrounded by concrete walkways and frequently mowed lawns
207 to avoid pollinations from outside plants. To allow pollinator access the plots in the

208 experimental garden were left open at the top (Zuppinger-Dingley et al. 2014). In a
209 subset of experimental communities, seed production in Zürich was not sufficient. In
210 those cases, additional seeds were collected directly in the plots of the Jena
211 Experiment (see Appendix S1: Table S6). The "selected" seeds were thus offspring of
212 plant populations that had been sown in 2002 and grown until 2010 in plots of the
213 Jena Experiment plus – for most of the seeds – one season in the experimental garden
214 in Zurich in the same species composition.

215 To make sure selected and naïve plants had similar starting conditions and to
216 reduce differential maternal carry-over effects between the two co-occurrence
217 histories, we germinated all seeds and propagated the resulting seedlings in a
218 glasshouse at the same time and under the same environmental conditions. In January
219 2011, the seeds were germinated in potting soil (BF4, De Baat; Holland) and in March
220 2011 the seedlings were transported to the Jena Experiment field site and transplanted
221 into 2 x 2 m smaller plots within the original large plots (see Fig. 1). There were four
222 1 x 1 m quadrats with different soil treatments in each 2 x 2 m plot (see next section)
223 and each quadrat was split into two 1 x 0.5 m halves. We planted seedlings of selected
224 communities into one half and seedlings of naïve communities into the other half of
225 each quadrat in a hexagonal pattern at a density of 210 plants per $m^2$ with a 6-cm
226 distance between individuals. By planting seedlings instead of sowing seeds, we
227 ensured equal abundances of species in the 141 pairs of 1 x 0.5 m subplots containing
228 the 282 test communities of different co-occurrence history, species diversity, and soil
229 treatments. After transplanting, the seedlings received water every second day for six
230 weeks.

231

232 **Soil treatments**

Within each 2 x 2 m plot of the 47 large plots of the Jena Experiment, we removed the original plant cover in September 2010 and used it for the plant propagation in the experimental garden in Zurich (see previous section). We excavated the soil to a depth of 0.35 m, added a 10-cm layer of sand to the bottom of the plots and covered it with a 0.5-mm mesh net. We separated the borders of the plots and the quadrats by plastic frames. The excavated native soil from each of the plots was sieved and four soil treatments were prepared. Half of the soil (approximately 600 kg per plot) was γ-irradiated to remove the original soil biota. Half of the sterilized soil was then inoculated with 4% (by weight) of live sugar-beet soil and 4% of sterilized native soil of the corresponding plot ("neutral soil" obtained by inoculation). We added live sugar-beet soil collected in an agricultural sugar-beet field not associated with the Jena Experiment, but with comparable soil properties to create a neutral soil community. The second half of the sterilized soil was inoculated with 4% (by weight) of live sugar-beet soil and 4% of live native soil of the corresponding plot ("native soil" obtained by inoculation). The non-sterilized part of the excavated soil was used for the second two soil treatments. Half of this soil was filled back into one quadrat of the corresponding plot ("native soil"). The other half of the unsterilized soil was mixed among all plots and filled into the remaining quadrats ("mixed soil"). However, this fourth soil treatment was destructively harvested for another experiment, which is why we excluded it from all analyses.

The soils were left to rest in closed bags to encourage soil biota of the inocula to colonize the sterilized soil before planting. The soils were then added into the quadrats in December 2010. We assessed whether the soil treatments remained distinct by taking samples in 2011 and 2012 (van Moorsel et al. 2018) and again in

2015. Differences in both soil chemistry and microbial composition between treatments were well maintained (Appendix S1: Table S4).

### Sampling of aboveground biomass

The plant communities were weeded three times a year and the plants were cut to 3 cm above ground twice a year. These harvests were conducted over an extended period of approximately two weeks at typical grassland harvest times (late May and August) in central Europe. Plant material from a 50 x 20 cm area in the center of each half-quadrat was collected to measure aboveground biomass. We sorted the biomass by species, dried it at 70°C and weighed the dried biomass. There were four May harvests (2012–2015) and three August harvests (2012–2014) because the experiment was terminated after the fourth May harvest in 2015.

### Flood event

In June 2013, the field site was flooded because of sustained heavy rains in central Europe (Blöschl et al. 2013, Wright et al. 2015). Due to heavy rainfall, a dam upstream of the Saale river was opened on 31 May, which resulted in a very fast influx of water to the field site and consequently standing water in the experimental plots. The flood duration (maximum 25 days) and depth of water (maximum of 40 cm) varied between 2 x 2 m plots but not between co-occurrence-history and soil treatments within plots (Fischer et al. 2016). Because flood severity (Wright et al. 2015) did not differentially influence any of the dependent variables in the present study (data not shown), we excluded flood severity indices from all analyses. The biomass harvest in May 2013 took place before the flood event from 20–30 May and was terminated once the flooding of the field site began (31 May). Eight plots located

282 closest to the river (three 8-species communities, three 2-species communities and
283 two 4-species communities) could not be harvested in time and the spring 2013
284 harvest data from these plots were therefore excluded from all analyses.
285
286 **Data analysis**
287 *Temporal stability of community biomass and climate*
288 To address hypothesis 1, we first calculated the stability of community aboveground
289 biomass as the inverse coefficient of combined intra- and inter-annual variation
290 ($CV_{com}^{-1}$) among sequential spring and summer harvests. The stability of a single
291 community was thus the mean community aboveground biomass ($\mu_{com}$) divided by its
292 standard deviation ($\sigma_{com}$). The basic sequence for this measure was spring year $n$,
293 summer year $n$, and spring year $n$+1, which had shown increasing stability during the
294 8 selection years in the Jena Experiment (2003/4, 2005/6, 2007/8, 2009/10; see
295 Appendix S1: Fig. S1A). This sequence allowed us to exclude the summer harvest
296 2013, which was taken two months after the flood event in August 2013 and was used
297 for the calculation of resistance and recovery (see below); and it increased the
298 independence of the sequential measures from 2003–2010. We calculated interannual
299 mean spring precipitation and temperature stability (Knapp 2001) for the same time
300 intervals in Jena (see Appendix S1: Fig. S1B).
301 We also analyzed pre-flood (first three harvests) and post-flood (last three
302 harvests) stability separately. Furthermore, we calculated the species compositional
303 turnover between pre- and post-flood conditions. Because it includes species
304 abundances, we used the Bray-Curtis dissimilarity between pre-flood (averaged over
305 the first three harvests) and post-flood abundances of species (averaged over the last
306 three harvests). Although the separate analyses of pre- and post-flood stabilities are

307 partly confounded with the analysis of overall stability across the three pre- and three
308 post-flood harvests, we did both types of analyses to focus on different aspects of
309 stability. Whereas the analysis of the overall stability as an integrative measure
310 allowed us to better estimate contributions of asynchrony and population stability to
311 community stability, the separate analyses of pre- and post-flood stabilities allowed us
312 to test if the flooding event not only affected resistance, recovery, and resilience of
313 communities (see below) but also the temporal stability over time in absence of
314 further perturbations.
315
316 *Population stability and species asynchrony*
317 We calculated average stability of biomass at the population level ($CV_{pop}^{-1}$) and
318 community-wise species biomass asynchrony ($1-\theta$) over the same time span as
319 overall stability. Stability of biomass at the population level was calculated as the
320 average stability of biomass of individual species (Thibaut and Connolly 2013).
321 Asynchrony was calculated as the "synchrony index" ($\theta$, Loreau and de Mazancourt
322 2008), which ranges between 0 and 1, thus, asynchrony is 1-$\theta$. For monocultures,
323 population stability equals community stability, and asynchrony is zero ($\theta$ is 1).
324 Because community stability is the product of population stability and the square root
325 of species synchrony (Thibaut and Connolly 2013, de Mazancourt et al. 2013), we
326 could assess the two components separately.
327
328 *Resistance, recovery, and resilience*
329 To address hypothesis 3, we calculated resistance, recovery, and resilience measures
330 (Schläpfer and Schmid 1999, Ruijven and Berendse 2010, Hillebrand et al. 2018) in
331 response to the flood event in 2013 (see Fig. 3). Resistance is the difference in

community biomass between the average of the three harvests before the flood and the community biomass two months after the flood (August 2013), more negative values indicating lower resistance. Recovery is the difference between the biomass produced after recovery from the flood (averaged over the three last harvests) and the biomass two months after the flood (August 2013), where positive values indicate the amount of biomass recovered. Resilience is the difference between the average biomass of the three harvests before the flood and the average biomass of the three harvests after recovery. Values close to zero or positive values indicate that communities had returned or overshot their pre-flood state, respectively, after the flood; and negative values indicate that post-flood biomass had not returned to its pre-flood state.

*Statistical analysis*

Variation in community stability, synchrony, and population stability was analyzed with linear mixed-effects models. Stability measures were log-transformed to improve homoscedasticity and obtain normally distributed residuals in the analyses (Schmid et al. 2017). Fixed-effects terms were plant species richness (log scale, addressing hypothesis 1), co-occurrence history (selected vs. naïve communities, addressing hypothesis 1), and soil treatment (native, inoculated-native, or inoculated-neutral soil, addressing hypothesis 2). Plots and quadrats were used as random-effects terms to get appropriate errors for significance tests (Schmid et al. 2017). We added all significant interactions of the fixed-effects terms as additional fixed-effects terms to the models (see Table 1). For reasons of consistency and to allow the use of all data in analyses with covariates, we included monocultures in the analysis of asynchrony. For graphical displays of relationships between species richness and stability measures

and asynchrony, means across soil treatments were corrected for differences between plots within species-richness levels, which corresponds to using plots and quadrats in the mixed-model analyses. Because co-occurrence history was a split-plot/split-quadrat treatment applied within each quadrat, it was not affected by the correction. The corrections were obtained by fitting a model with plots and quadrats only and adding the residuals to the diversity-level means.

Variation in resistance, recovery, and resilience was also analyzed with the same linear mixed-effects models as described above. Since the measures of resistance, recovery, and resilience can depend on the magnitude of the pre-flood biomass (Pfisterer and Schmid 2002, Wright et al. 2015), we analyzed additional models, which included the average of the three harvests before the flood as covariate (see Appendix S1: Table S1).

To assess the magnitude of the plant community response to either biodiversity or co-occurrence, we calculated percentage sum of squares (%SS) as effect sizes using general linear models (Schmid et al. 2017). The total SS of all fixed-effects terms was defined as 100% SS (see Appendix S1: Fig. S3). All analyses were conducted using the software R, version 3.2.4 (R Development Core Team 2017). Mixed models using residual maximum likelihood (REML) were fitted using the package ASReml for R (Butler 2009) and the package 'Pascal' available at GitHub (Schmid et al. 2017).

## RESULTS

### Co-occurrence history partially compensates the negative effects of biodiversity loss on biomass stability

Community biomass stability across pre-flood and post-flood harvests increased with

species richness (Figure 2A, Table 1). Differences in community biomass stability between soil treatments were insignificant (Table1). Differences between selected and naïve communities (co-occurrence treatment) were small, however, at low diversity, selected communities were more stable than naïve communities, reflected by a significant co-occurrence history x species richness interaction (Table 1; Fig. 2A).

Population biomass stability decreased with species richness, but at low diversity, the population biomass stability was also greater in selected communities (Table 1; Fig. 2B). In contrast, species asynchrony in terms of biomass increased for both selected and naïve communities with increasing species richness (Table 1; Fig. 2C). When we corrected community stability and species asynchrony for all model terms except co-occurrence history (i.e. taking residuals after fitting the plot x soil treatment interaction), stability residuals strongly increased with asynchrony residuals ($P < 0.001$). Selected communities were consistently more stable than naïve communities ($P < 0.01$; Fig. 2D). An analysis of effect sizes showed that log-transformed richness had the strongest effect (between 77 and 99%, Appendix S1: Fig. S3A) on community stability, population stability, and asynchrony.

**Diverse communities were less resistant to a flood event but recovered better**

A flood in early summer 2013 strongly reduced biomass in that summer (Fig. 3 and Appendix S1: Fig. S2). However, in contrast to the main plots in the Jena Experiment (Wright et al. 2015), the flood did not interfere with the positive diversity–community biomass stability relationship in our plots (Fig. 5). In the short term, diverse communities, especially selected ones, were the least resistant (Fig. 4A). At low diversity, selected communities tended to have greater resistance than naïve communities, especially when adjusting for community biomass before the flood (by

407 adding pre-flood biomass as a term in the model, see Appendix S1: Table S1; Fig.
408 S4A).

409 Plant communities in the non-sterilized native soil had the lowest biomass
410 prior to the flood, lost the smallest amount that summer, and were thus most resistant
411 (Fig. 3B). In contrast, plant communities grown in neutral soil had the highest
412 biomass prior to the flood and were the least resistant to the flood resulting in a
413 significant effect of soil treatment on resistance (Table 2; Fig. 3B). However, after
414 first accounting for the pre-flood biomass, there were no effects of soil treatments on
415 resistance (Appendix S1: Table S1).

416 Recovery of community biomass after the flood increased with species
417 richness and was greater in selected than in naïve communities across all diversity
418 levels and soil treatments (Table 2 and Appendix S1: Table S1; Fig. 4B and Appendix
419 S1: Fig. S2B). Selected communities were also more resilient than naïve
420 communities, as shown by the comparison of community biomass before and after
421 recovery (Fig. 3A), and particularly at low diversity (Fig. 4C). However, the effect of
422 co-occurrence on resilience was only significant if adjusted for pre-flood community
423 biomass (Table 2 and Appendix S1: Table S1; Fig. 4C and Appendix S1: Fig. S4C).
424 The three soil treatments strongly differed in their resilience, which averaged out their
425 pre-flood differences in community biomass (Table 2; Fig. 3B).

426 Effect sizes (%SS) showed that species richness had the strongest impact on
427 resistance (42%), the interaction between soil history and species richness the
428 strongest impact on recovery (37%) and species richness the strongest impact on
429 resilience (70%, Appendix S1: Fig. S3B). Co-occurrence history contributed with
430 23% to resilience.

431

### Selected communities were more stable after the flood

We compared the combined intra- and interannual biomass stability over the first three harvests before the flood event (2012–2013, Fig. 5A) with the last three harvests after recovery (2014–2015, Fig. 5B). Before the flood, selected communities were not significantly more stable than naïve communities (Appendix S1: Table S2). After the flood event, the selected communities were consistently more stable than the naïve communities across all diversity levels (Appendix S1: Table S2). Lastly, species turnover rates (Bray-Curtis similarity) between pre-and post-flood species compositions were not influenced by co-occurrence history or soil treatments, although they increased with species richness (Appendix S1: Table S3 and Fig. S5).

## DISCUSSION

We previously found that, in comparison with naïve communities, selected low-diversity mixtures were more productive but this was not the case for selected higher-diversity mixtures (van Moorsel et al. 2018). Here, we show that selected communities from the Jena Experiment also showed greater community biomass stability in comparison with naïve communities, particularly at low diversity.

Temporal stability in terms of biomass at the community level in grassland ecosystems can be driven by asynchronous population dynamics of species, allowing high compensatory population variation to be combined with low community-level variation over time (Flynn et al. 2008, Isbell et al. 2009, Hector et al. 2010, de Mazancourt et al. 2013, Gross et al. 2014). As shown before (e.g. Tilman et al. 2006), we found that community biomass stability increased but population biomass stability decreased with increasing species richness. However, this effect of species richness on population stability was weaker in naïve communities (see Fig. 2B), suggesting

457 that adaptation to the abiotic environment partially compensated for the reduced
458 species richness over time, especially in monocultures and low-diversity mixtures. In
459 low-diversity mixtures, population stability could also have been increased due to
460 reduced competitive interactions between plant species, consistent with the findings
461 of evolutionary niche differentiation (Zuppinger-Dingley et al. 2014) and increased
462 facilitation (Schöb et al. 2018) among species in mixtures in the Jena Experiment. By
463 extension, similar evolutionary processes may have occurred between genotypes
464 within monocultures, again consistent with previous findings showing evolutionarily
465 changed phenotypic variation within monocultures after eight years of selection in the
466 Jena Experiment (van Moorsel et al. 2018). The evolution of reduced inter- and
467 intraspecific competition and parallel adaptations among the multiple species to the
468 local abiotic conditions are mutually non-exclusive explanations for the increased
469 population stability at low diversity. Because community stability is the product of
470 species stability and species synchrony (Thibaut & Connolly, 2013), yet asynchrony
471 did not differ between selected and naïve communities (see Fig. 2C), we conclude that
472 asynchrony did not contribute to the greater community stability of selected
473 communities at low diversity.
474
475 **Selected communities at low diversity are more stable and recover better from**
476 **disturbance**
477 Diverse communities are more stable in the face of disturbances (Isbell et al.
478 2015), such as a flood as happened to our test communities halfway through the
479 experiment in June 2013 (Wright et al. 2015). Considering predicted future climate
480 scenarios with increased frequency of extreme events (Stocker et al. 2013), including
481 floods (Hirabayashi et al. 2013), this aspect of stability may even be more relevant

than temporal stability under unperturbed conditions (Donohue et al. 2016).

In our experiment, diversity reduced ecosystem resistance in the short term, in line with previous findings for example in micro-ecosystems with ciliates responding to warming (Pennekamp et al. 2018). This was because 4- and 8-species communities had more biomass before the flood and lost more biomass (in absolute terms), a result found previously for community responses to drought (Pfisterer and Schmid 2002, Wang et al. 2007, Ruijven and Berendse 2010) and flood (Wright et al. 2015). Because selected communities were additionally more productive than naïve communities at the 8-species richness level, naïve communities were more resistant than selected communities as they had less to lose (see Fig. 4A). Diverse communities made up for their reduced resistance by increased recovery, as often found in biodiversity experiments (Ruijven and Berendse 2010, Lloret et al. 2011, but see Isbell et al. 2015). Remarkably, however, selected communities showed greater recovery than naïve communities along the entire species-richness gradient. In combination, the differential responses regarding resistance and recovery caused selected communities at low diversity to be more resilient than naïve communities, whereas no differences in resilience between selected and naïve communities were observed at higher diversity (see Fig. 4C).

Some communities, mostly selected 2- and 4-species communities and both selected and naïve 8-species communities, were more productive after the flood than ever before (reflected in the positive resilience values shown in Fig. 4C). This could have been due to several potential non-exclusive causes: 1) continued accumulation of belowground biomass potentially less affected by flooding (and greater in selected than in naïve communities), 2) relative accumulation of beneficial microbes in comparison to plant antagonistic microbes (especially in sterilized soil treatments), 3)

507 resource enrichment associated with the flood (as suggested by Wright et al. 2015).
508 Accumulation of beneficial soil microbes seems to play a minor role though because
509 soil treatments did not differentially affect selected vs. naïve communities. However,
510 selected communities may have been able to benefit more from resource enrichment
511 because they had evolved better division of labor (Zuppinger-Dingley et al. 2014).
512 Such an evolutionary driven trait divergence would have increased functional
513 diversity which has been shown to contribute to greater stability in response to
514 extreme climatic events (de la Riva et al. 2017).
515 Whereas the differences in community temporal biomass stability between
516 selected and naïve communities were only positive in monocultures before the flood
517 (see Fig. 5A), the selected communities showed increased post-flood stability at all
518 diversity levels (see Fig. 5B and Appendix S1: Table S2). This was driven by the
519 improved recovery of the selected communities which resulted in a larger increase in
520 mean biomass (van Moorsel et al. 2018) than in temporal variation of biomass and a
521 consequently reduced CV of biomass. This improved stability of selected
522 monocultures and mixtures after the flood event was likely due to local adaptation of
523 plants to the abiotic conditions at the Jena field site, a natural floodplain. The plant
524 communities were exposed to previous milder flood events in winter 2003 and winter
525 2005 (personal communication with C. Roscher) which selected for individuals with
526 traits that allowed them to recover more rapidly (Garssen et al. 2015, Wright et al.
527 2017). The contribution of such parallel evolutionary responses among the multiple
528 species of our experiment to their abiotic environment was reflected in their increased
529 population stability at low diversity (see Fig. 2B) and the consistently greater stability
530 of selected communities across the entire range of species asynchronies (see Fig. 2D).
531 However, in mixtures, adaptation to the biotic environment, i.e. species interactions,

must also have been involved because the differences between selected and naïve communities depended on diversity.

Because we did not detect any altered species abundance distributions (Vogel et al. 2019), it seems likely that changes in genotype frequencies within species, i.e. evolution in the community context (Strauss et al. 2006), contributed to increased stability. Genetic analyses on a subset of five species from the Jena Experiment confirmed for one annual species and two perennial species the potential for such rapid evolutionary changes and their genetic basis, with consequential epigenetic and phenotypic changes (van Moorsel et al. 2019). Furthermore, we found quantitative-genetic divergence in eleven species (Zuppinger-Dingley et al. 2014). The changes in genotype frequencies within species in selected communities could be attributable to differential mortality, growth, or reproduction among the initially sown genotypes (Barrett and Schluter 2008), recombination during sexual reproduction or, least likely, to mutation. An additional explanation for the observed patterns could be a physiological process in perennial species, i.e. priming to abiotic stress (Conrath et al. 2006). Perennial individuals may be more capable of producing flood-resistant structures due to priming earlier in their lives. However, even in this case there would have been a difference between selected and naïve communities in priming, again suggesting evolution in low-diversity communities after simulated species loss in the original field experiment.

**Diverse communities were more stable regardless of co-occurrence history**

At the highest diversity level, differences between selected and naïve communities were small and only visible in the more negative resistance, the more positive recovery, and in the greater post-flood stability. This result mirrors earlier findings for

557 productivity, where mean yearly biomass was similar for selected and naïve
558 communities at the 8-species richness level (van Moorsel et al. 2018). Potential
559 effects of co-evolution may be weaker at higher diversity with less consistent and
560 stable interactions between particular species (Connell 1980, van Moorsel et al. 2018).
561 Stronger selective pressure between particular species leading to co-evolution could
562 explain why the differences between selected and naïve communities were stronger at
563 lower diversity, especially in 2- and 4-species mixtures. The increased resilience of
564 selected communities at the lower diversity levels may in part also have been driven
565 by evolutionarily increased facilitation (Bronstein 2009), which has been
566 demonstrated for these plants in the Jena Experiment (Schöb et al. 2018). This would
567 be in line with predictions that environmental stress might select for more positive
568 interactions between species in plant communities (Callaway et al. 2002).
569 Resilience was slightly overshooting at the 8-species richness level (Fig. 4C),
570 which indicates that species richness *per se* is already beneficial in the way that at
571 lower richness, communities, in general, were not fully resilient. The increased
572 resilience in selected and naïve 8-species communities was driven by a high recovery
573 that overshot pre-flood levels of biomass production, which may have been aided by
574 the same causes as those mentioned in the previous section, namely higher
575 belowground biomass or greater resource enrichment in more diverse communities.
576 However, in contrast to Wright et al. (2015), we found that flooding did not decrease
577 community stability and that after flooding diverse communities were still more stable
578 than less diverse communities. Some of these dissimilarities between the two studies
579 might have been due to different calculations of stability measures, species diversity
580 gradients and managements of experimental plots.
581

## Influence of associated soil organisms

Soil communities can strongly affect biodiversity effects in plant communities. Specifically, for the Jena Experiment, previous findings suggested differential evolution of plant–soil feedbacks in monocultures vs. mixtures (Zuppinger-Dingley et al. 2016). Therefore, we designed our experiment with three soil treatments to detect possible effects of associated microbial communities on community stability. However, we could not find any interactions between them and plant community co-occurrence history. Based on this "negative" result, we tentatively conclude that our above interpretations about plant evolutionary changes due to co-occurrence history were not confounded by a differential assembly of soil communities over time in the Jena Experiment. That the soil treatments did work in principle could be seen by the main effects. Pre-flood productivity was lower when native soil biota were present, which could have been due to a greater density of antagonistic soil biota in native and native-inoculated soils (Schnitzer et al. 2011), or a greater pool of available soil resources resulting from the soil sterilization process in the two inoculated soils (Gebremikael et al. 2015). Recovery and resilience were greater for communities growing in native soil (see Fig. 3B), suggesting that native soil organisms did have a beneficial effect on both selected and naïve plant communities after they had been affected by the flood event.

## Conclusions

So far, evolutionary mechanisms underlying ecosystem stability in biodiversity experiments have only been studied in terms of phylogenetic relatedness that reflects evolutionary processes over long time scales, with conflicting results (e.g., Cadotte et al. 2012, Venail et al. 2015). Experimental evidence for short-term evolution leading

607 to changes at the community level, referred to as community evolution (van Moorsel
608 et al. 2018), has been reported for microbial ecosystems (Gravel et al. 2011, Lawrence
609 et al. 2012, Fiegna et al. 2014, 2015, Zhao et al. 2016). However, short-term
610 evolutionary processes could be particularly relevant in plant communities facing
611 rapid global change (Schmid et al. 1996, Davis et al. 2005) because plants are fixed in
612 place and can only move by propagule dispersal. Here we show that evolution can
613 affect biomass stability after only 8 years and a few generations of sexual
614 reproduction in communities of perennial plant species, likely due to sufficient
615 "standing genetic variation" (Fakheran et al. 2010) in the original seed populations
616 (van Moorsel et al. 2019). At low diversity, communities could compensate with
617 evolutionary adjustments resulting in a better occupation of the available niche space
618 either via evolved (genetic) trait divergence or evolved trait plasticity (Zuppinger-
619 Dingley et al. 2014, Meilhac et al. 2020). In more complex and diverse communities,
620 opportunities for community evolution may be more restricted due to weaker
621 interactions between particular species (Fox 1988) and because the community niche
622 (Salles et al. 2009) is already large due to "random" differences between species. In
623 this sense, we speculate that communities may either be stabilized by co-evolution
624 between few species or diversity of many species, both leading to greater trait
625 diversity. We encourage others with long-term biodiversity experiments to do similar
626 follow-up experiments. Comparable results from biodiversity experiments around the
627 globe will strengthen the hypothesis that selection in a community context can
628 increase stability, which would have far-reaching consequences for the fields of
629 conservation and restoration ecology.
630

631 **LITERATURE CITED**
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## Additional information

**Supplementary information** is available for this paper online.

**Data and code availability.** Data and code (R scripts) are available from the corresponding author and will be made publicly available upon acceptance on the Pangaea repository.


## Acknowledgements

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## Author contributions

B.S. designed research, T.H. and S.J.V.M. performed research; A.E. and N.E. maintained and coordinated the field site; S.J.V.M., C.W. and B.S. analyzed data; S.J.V.M., B.S., O.L.P. and C.W. wrote the paper. All co-authors contributed to subsequent versions of the paper.

## Competing interests

The authors declare no conflicts of interest.

**TABLE 1. Mixed-model ANOVA results for log-transformed community stability, log-transformed mean population stability and untransformed asynchrony.**

| | | Stability ($CV^{-1}$) | | | Population stability ($CV_{pop}^{-1}$) | | | Asynchrony ($1-\theta$) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fixed terms | $DF_{num}$ | $DF_{den}$ | $F$ | $P$ | $DF_{den}$ | $F$ | $P$ | $DF_{den}$ | $F$ | $P$ |
| Log richness ($R_{log}$) | 1 | ***44.1*** | ***10.74*** | ***0.002*** | ***44.1*** | ***5.27*** | ***0.027*** | ***44.1*** | ***143.00*** | ***<0.001*** |
| Soil treatment (SH) | 2 | 87.1 | 0.64 | 0.529 | 87.1 | 1.30 | 0.278 | 87.1 | 0.87 | 0.424 |
| Co-occurrence history (CH) | 1 | 135.0 | 1.80 | 0.181 | 135.0 | 3.79 | 0.054 | 135.0 | 0.50 | 0.479 |
| SH x $R_{log}$ | 2 | 87.2 | 0.05 | 0.954 | 87.2 | 0.01 | 0.992 | 87.2 | 0.38 | 0.685 |
| CH x $R_{log}$ | 1 | ***135.0*** | ***4.79*** | ***0.030*** | ***135.0*** | ***8.38*** | ***0.004*** | 135.0 | 0.05 | 0.830 |
| Random terms | $N$ | *Var.* $10^{-3}$ | *SE* $10^{-3}$ | | *Var.* $10^{-3}$ | *SE* $10^{-3}$ | | *Var.* $10^{-3}$ | *SE* $10^{-3}$ | |
| Plot | 46 | 100.1 | 25.9 | | 95.6 | 23.5 | | 17.9 | 4.6 | |
| Plot x SH | 137 | 15.5 | 10.9 | | 13.9 | 7.4 | | -0.1 | 2.0 | |
| Residual | 274 | 92.3 | 11.2 | | 58.4 | 7.1 | | 20.0 | 2.5 | |

*Notes*: The effects of species richness (log scale), soil treatments, and co-occurrence history on the stability of community and population biomass and on asynchrony across the entire experimental period from 2012–2015 were analyzed (excluding the time point immediately after the extreme event of a late spring flood in June 2013). Significant effects are highlighted in bold. $DF_{num}$ = numerator degrees of freedom, $DF_{den}$ = denominator degrees of freedom, $F$ = variance ratio, $P$ = probability of type-I error.

**TABLE 2. Mixed-model ANOVA results for resistance, recovery, and resilience of community biomass in response to the extreme event of a late spring flood in June 2013.**

| | | Resistance | | | Recovery | | | Resilience | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fixed terms | $DF_{num}$ | $DF_{den}$ | $F$ | $P$ | $DF_{den}$ | $F$ | $P$ | $DF_{den}$ | $F$ | $P$ |
| Log richness ($R_{log}$) | 1 | ***44.2*** | ***9.41*** | ***0.004*** | ***44.1*** | ***15.95*** | ***<0.001*** | 44.2 | 1.69 | 0.200 |
| Soil treatment (SH) | 2 | ***87.3*** | ***14.07*** | ***<0.001*** | 87.2 | 0.29 | 0.745 | ***87.3*** | ***6.12*** | ***0.003*** |
| Co-occurrence history (CH) | 1 | ***135*** | ***4.19*** | ***0.043*** | ***135*** | ***14.50*** | ***<0.001*** | 135 | 3.48 | 0.064 |
| SH x $R_{log}$ | 2 | ***87.5*** | ***5.95*** | ***0.004*** | 87.4 | 1.73 | 0.184 | ***87.5*** | ***6.97*** | ***0.002*** |
| CH x $R_{log}$ | 1 | ***135*** | ***5.32*** | ***0.023*** | 135 | 0.48 | 0.488 | 135 | 2.65 | 0.106 |
| Random terms | $N$ | *Var.* | *SE* | | *Var.* | *SE* | | *Var.* | *SE* | |
| Plot | 46 | 3645 | 1074 | | 2234 | 771 | | 6910 | 2238 | |
| Plot x SH | 137 | 775 | 702 | | -158 | 745 | | 1933 | 1784 | |
| Residual | 274 | 6246 | 760 | | 7851 | 956 | | 15914 | 1937 | |

*Notes*: The effects of species richness (log scale), soil treatments, and co-occurrence history on responses of community biomass to flooding were analyzed. Bold italic text highlights significant effects. (Similar ANOVAs with pre-flood biomass as covariate are shown in Appendix S1: Table S3.) $DF_{num}$ = numerator degrees of freedom, $DF_{den}$ = denominator degrees of freedom, $F$ = variance ratio, $P$ = probability of type-I error.

948 **FIGURE CAPTIONS**

949

950 **FIG. 1. Experimental set-up of plant communities in the field.** Seeds from plants
951 that had been co-occurring for eight years in 47 plots of the Jena Experiment (selected
952 plants) and seeds purchased from a seed supplier (naïve plants) were germinated at
953 the same time in a glasshouse. These seedlings were then transplanted back to the
954 Jena field site in March 2011 according to randomized planting schemes with equal
955 species composition and abundances. Selected (light green) and of naïve communities
956 (dark green) were grown, in the same 47 plots from which selected plants had been
957 taken, in four quadrats separated by plastic frames with different soil treatments
958 (unsterilized native or mixed soil or sterilized soil with native or neutral inoculum, see
959 Methods). The mixed-soil treatment was not used in this paper because it was
960 harvested early for a different experiment. Co-occurrence history (selected vs. naïve)
961 was thus a split-split plot treatment replicated for 47 community compositions
962 (including 11 monocultures) times three soil treatments. We ensured equal
963 abundances and positions of species in the 141 pairs of 1 x 0.5 m subplots (see
964 planting scheme).

965

966 **FIG. 2. The biodiversity–stability relationship for selected (blue) and naïve**
967 **communities (red). (A)** Community stability, (**B)** mean population stability, **(C)**
968 asynchrony, **(D)** relationship between stability and asynchrony after correction for all
969 other model terms except co-occurrence history. The corrections were obtained by
970 fitting a model with plots and quadrats only and adding the residuals to the diversity-
971 level means (see Methods). Colored bands show standard errors of predictions from
972 mixed models as presented in Table 1. For significances see Table 1 (panels A–C);
973 the slopes in panel D are significant at $P < 0.001$. In panels A–C points are means of

974 the three soil treatments estimated from the model in Table 1. Points in D are residual
975 values of each plant community after accounting for the variation due to soil
976 treatments, planted richness, and plot identity.
977
978 **FIG. 3. Plant community biomass before and after the flood event.** Points indicate
979 the average community biomass across all diversity levels for **(A)** selected (blue) and
980 naïve communities (red) and **(B)** native soil (blue), sterilized soil with native
981 inoculum ("inoculated", green) and sterilized soil with neutral inoculum ("neutral",
982 orange). Resistance is the difference in biomass between the average of the three
983 harvests before the flood (May 2012, August 2012, and May 2013) and the biomass
984 directly after the flood (label "Flood" on x-axis corresponding to summer harvest in
985 August 2013). Recovery is the difference in biomass between the average of the three
986 harvests after recovery from the flood (May 2014, August 2014, and May 2015) and
987 the biomass directly after the flood ("Flood" label). Resilience is the difference in
988 biomass between the average of the three harvests after recovery from the flood and
989 the average of the three harvests before the flood. See also Appendix S1: Figure S2.
990 Means and standard errors were calculated from raw data.
991
992 **FIG. 4. Resistance, recovery, and resilience to the flood event. (A)** Biodiversity–
993 resistance relationships, **(B)** biodiversity–recovery relationships, and **(C)**
994 biodiversity–resilience relationships for selected (blue) and naïve communities (red).
995 Colored bands show standard errors of predictions from mixed models as presented in
996 Table 2. For significances see Table 2. Points are means of the three soil treatments
997 estimated from the model in Table 2. The dashed line at 0 indicates no change in
998 biomass in response to the flood (resistance), after the flood (resistance), or between

pre- and post-flood harvests (resilience). Similar plots with values corrected for variation in pre-flood biomass as covariate are shown in Appendix S1: Fig. S3.

**FIG. 5. The biodiversity–stability relationship for selected (blue) and naïve communities (red). (A)** The three harvests before the extreme event of a late spring flood in June 2013 and **(B)** the three harvests after recovery from the flood. Colored bands show standard errors of predictions from mixed models as presented in Appendix S1: Table S2. $P < 0.001$ for the effect of log richness in post-flood stability and $P = 0.027$ for the effect of co-occurrence history on post-flood stability. For other test-statistics see Appendix S1: Table S2. Points are means of the three soil treatments estimated from the model in Appendix S1: Table S2.

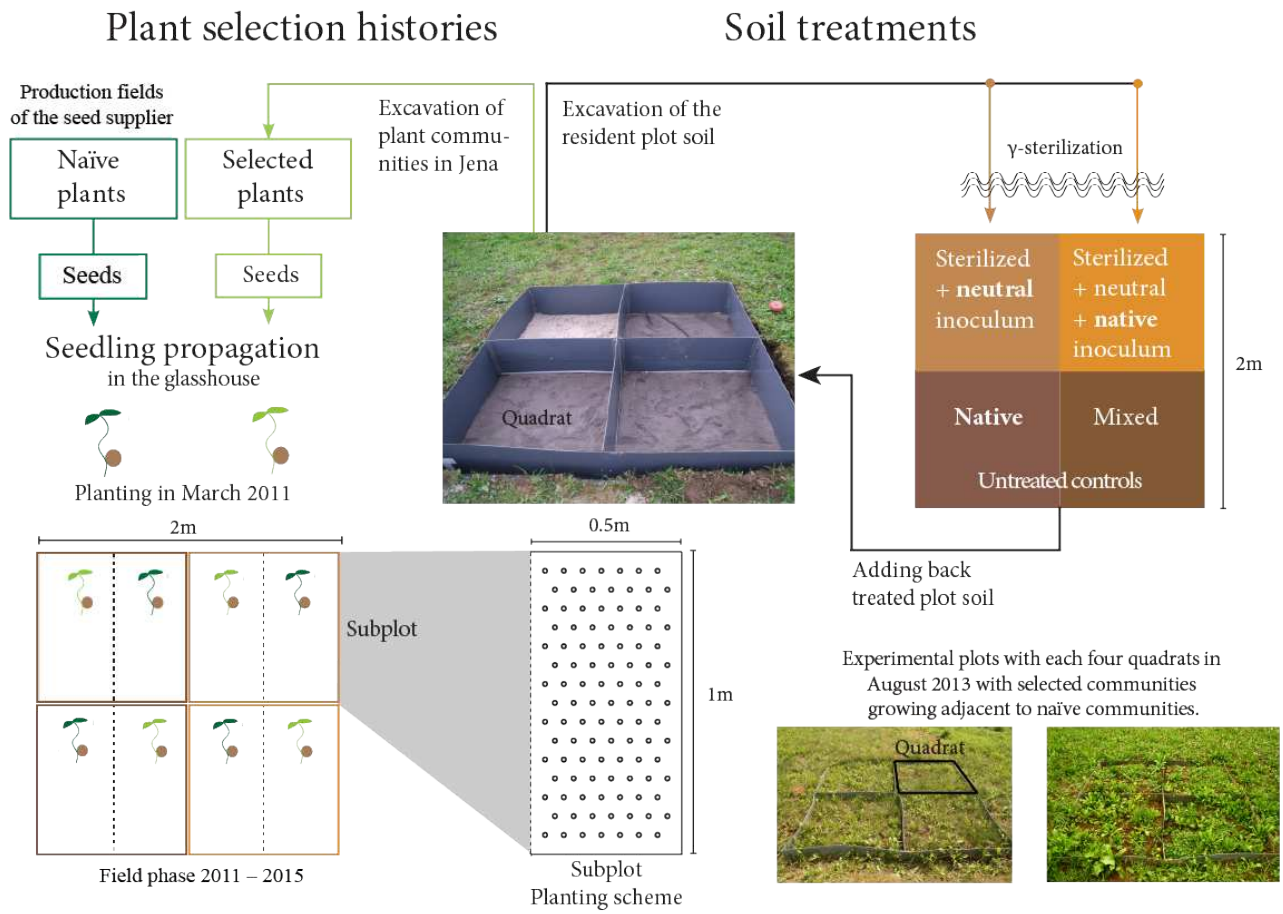


**FIG. 1. Experimental set-up of plant communities in the field.** Seeds from plants that had been co-occurring for eight years in 47 plots of the Jena Experiment (selected plants) and seeds purchased from a seed supplier (naïve plants) were germinated at the same time in a glasshouse. These seedlings were then transplanted back to the Jena field site in March 2011 according to randomized planting schemes with equal species composition and abundances. Selected (light green) and of naïve communities (dark green) were grown, in the same 47 plots from which selected plants had been taken, in four quadrats separated by plastic frames with different soil treatments (unsterilized native or mixed soil or sterilized soil with native or neutral inoculum, see Methods). The mixed-soil treatment was not used in this paper because it was harvested early for a different experiment. Co-occurrence history (selected vs. naïve) was thus a split-split plot treatment replicated for 47 community compositions (including 11 monocultures) times three soil treatments. We ensured equal abundances and positions of species in the 141 pairs of 1 x 0.5 m subplots (see planting scheme).

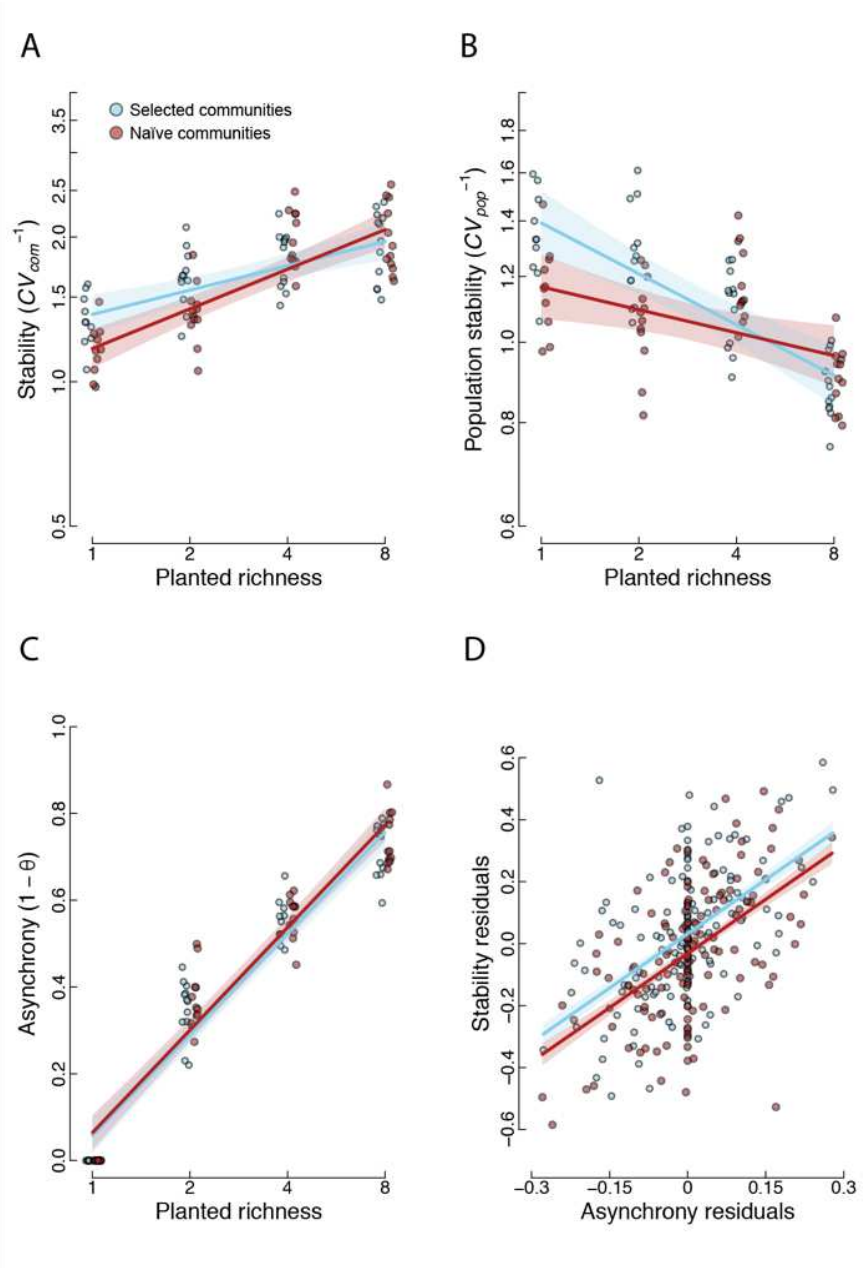


**FIG. 2. The biodiversity–stability relationship for selected (blue) and naïve communities (red). (A)** Community stability, **(B)** mean population stability, **(C)** asynchrony, **(D)** relationship between stability and asynchrony after correction for all other model terms except co-occurrence history. The corrections were obtained by fitting a model with plots and quadrats only and adding the residuals to the diversity-level means (see Methods). Colored bands show standard errors of predictions from mixed models as presented in Table 1. For significances see Table 1 (panels A–C); the slopes in panel D are significant at $P < 0.001$. In panels A–C points are means of the three soil treatments estimated from the model in Table 1. Points in D are residual values of each plant community after accounting for the variation due to soil treatments, planted richness, and plot identity.

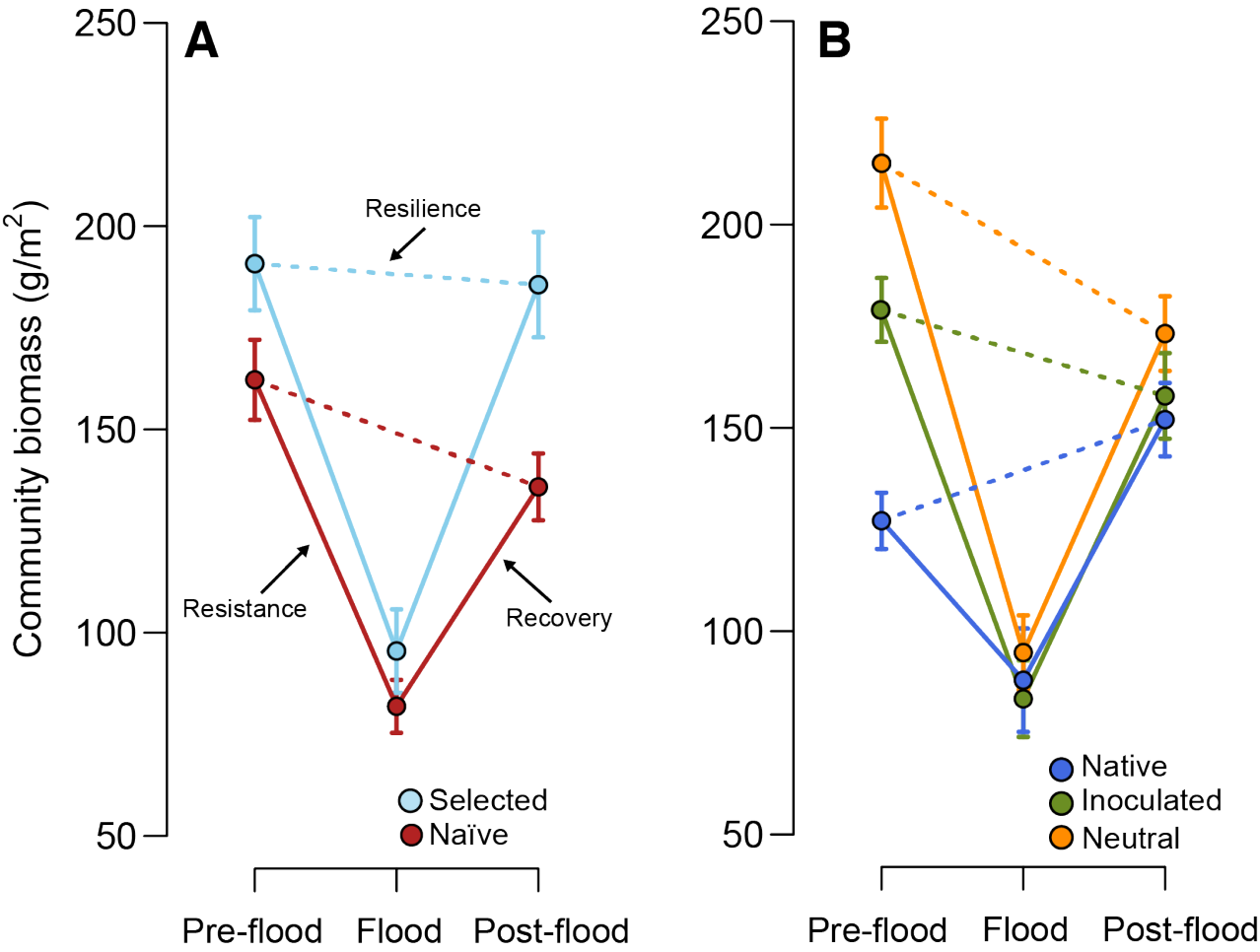


**FIG. 3. Plant community biomass before and after the flood event.** Points indicate the average community biomass across all diversity levels for **(A)** selected (blue) and naïve communities (red) and **(B)** native soil (blue), sterilized soil with native inoculum ("inoculated", green) and sterilized soil with neutral inoculum ("neutral", orange). Resistance is the difference in biomass between the average of the three harvests before the flood (May 2012, August 2012, and May 2013) and the biomass directly after the flood (label "Flood" on x-axis corresponding to summer harvest in August 2013). Recovery is the difference in biomass between the average of the three harvests after recovery from the flood (May 2014, August 2014, and May 2015) and the biomass directly after the flood ("Flood" label). Resilience is the difference in biomass between the average of the three harvests after recovery from the flood and the average of the three harvests before the flood. See also Figure Appendix S1: S2. Means and standard errors were calculated from raw data.

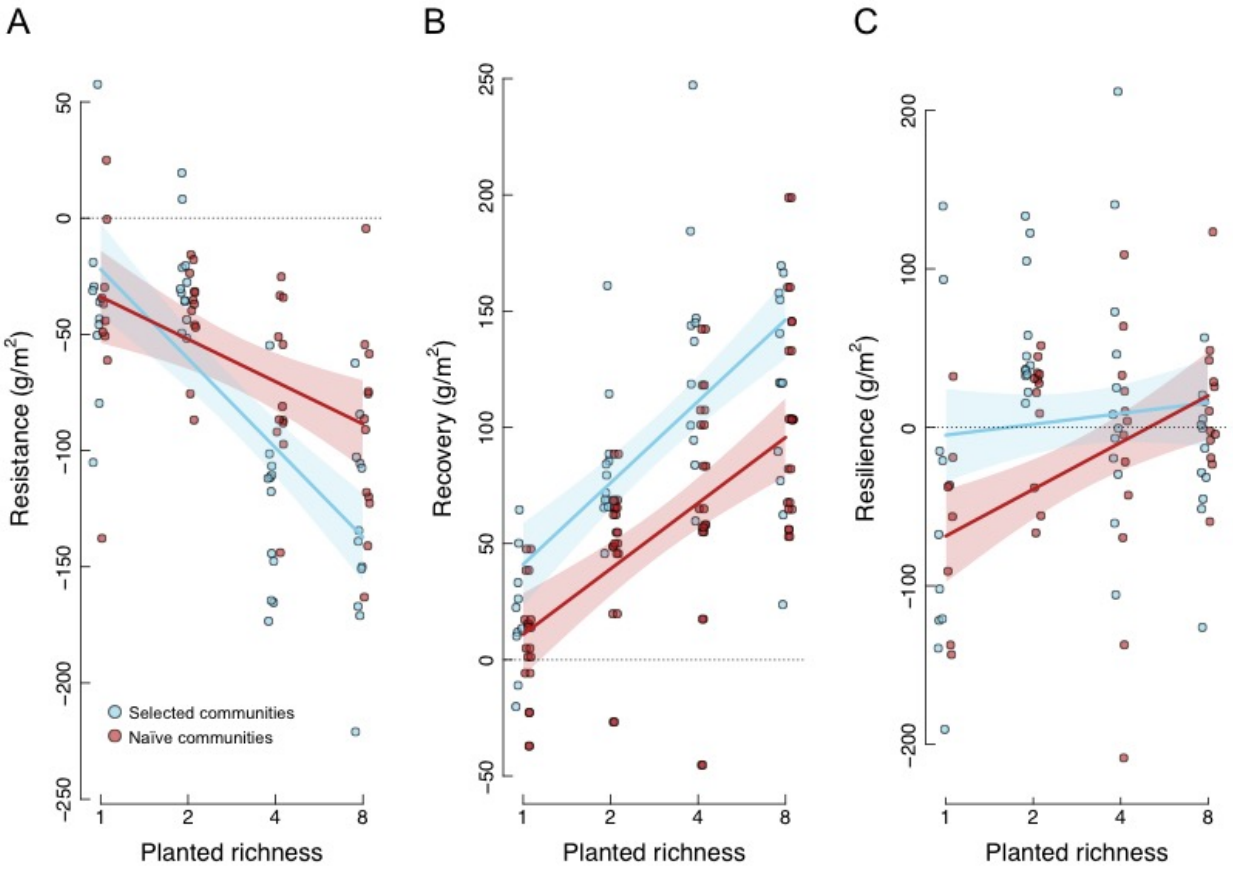


**FIG. 4. Resistance, recovery, and resilience to the flood event. (A)** Biodiversity–resistance relationships, **(B)** biodiversity–recovery relationships, and **(C)** biodiversity–resilience relationships for selected (blue) and naïve communities (red). Colored bands show standard errors of predictions from mixed models as presented in Table 2. For significances see Table 2. Points are means of the three soil treatments estimated from the model in Table 2. The dashed line at 0 indicates no change in biomass in response to the flood (resistance), after the flood (resistance), or between pre- and post-flood harvests (resilience). Similar plots with values corrected for variation in pre-flood biomass as covariate are shown in Appendix S1: Fig. S3.

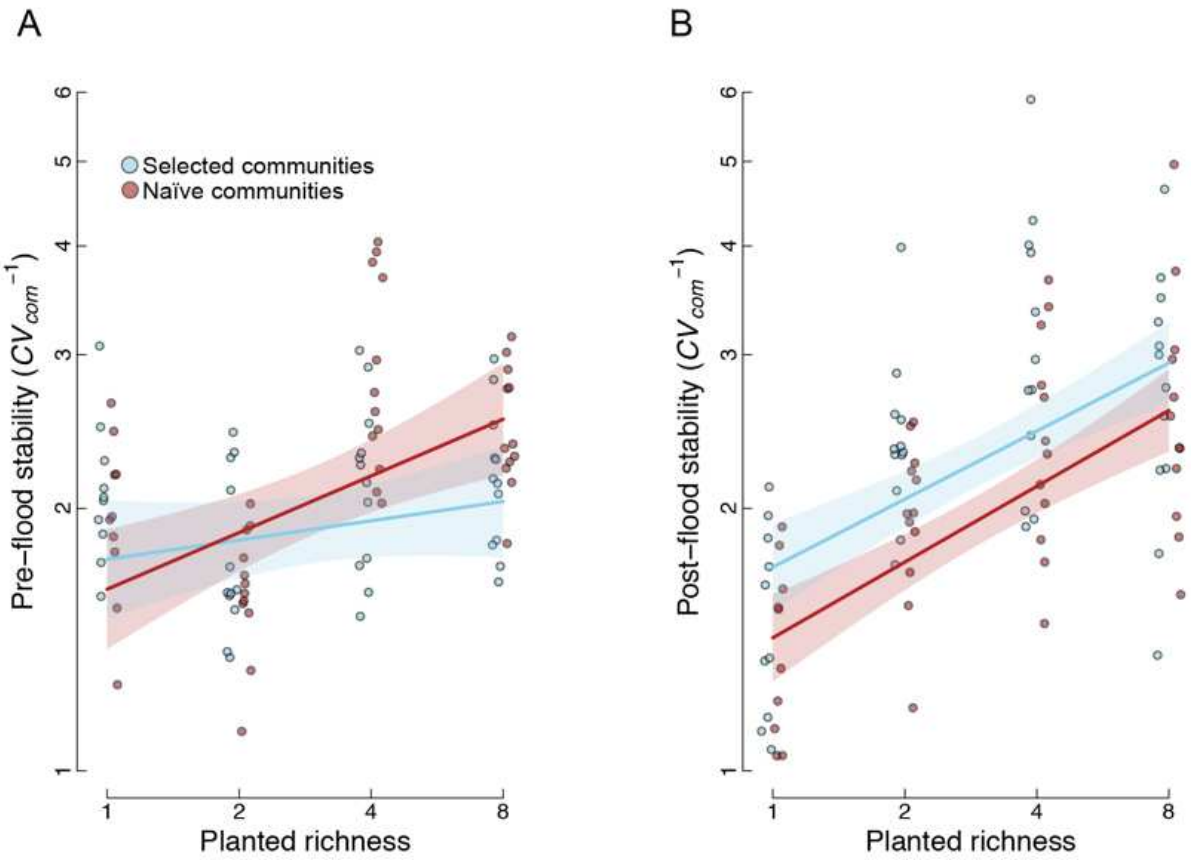


**FIG. 5. The biodiversity–stability relationship for selected (blue) and naïve communities (red). (A)** The three harvests before the extreme event of a late spring flood in June 2013 and **(B)** the three harvests after recovery from the flood. Colored bands show standard errors of predictions from mixed models as presented in Appendix S1: Table S2. $P < 0.001$ for the effect of log richness in post-flood stability and $P = 0.027$ for the effect of co-occurrence history on post-flood stability. For other test-statistics see Appendix S1: Table S2. Points are means of the three soil treatments estimated from the model in Appendix S1: Table S2.

**Ecology**

**Appendix S1 for:**

# Co-occurrence history increases ecosystem stability and resilience in experimental plant communities

Sofia J. van Moorsel, Terhi Hahl, Owen L. Petchey, Anne Ebeling, Nico Eisenhauer, Bernhard Schmid, and Cameron Wagg

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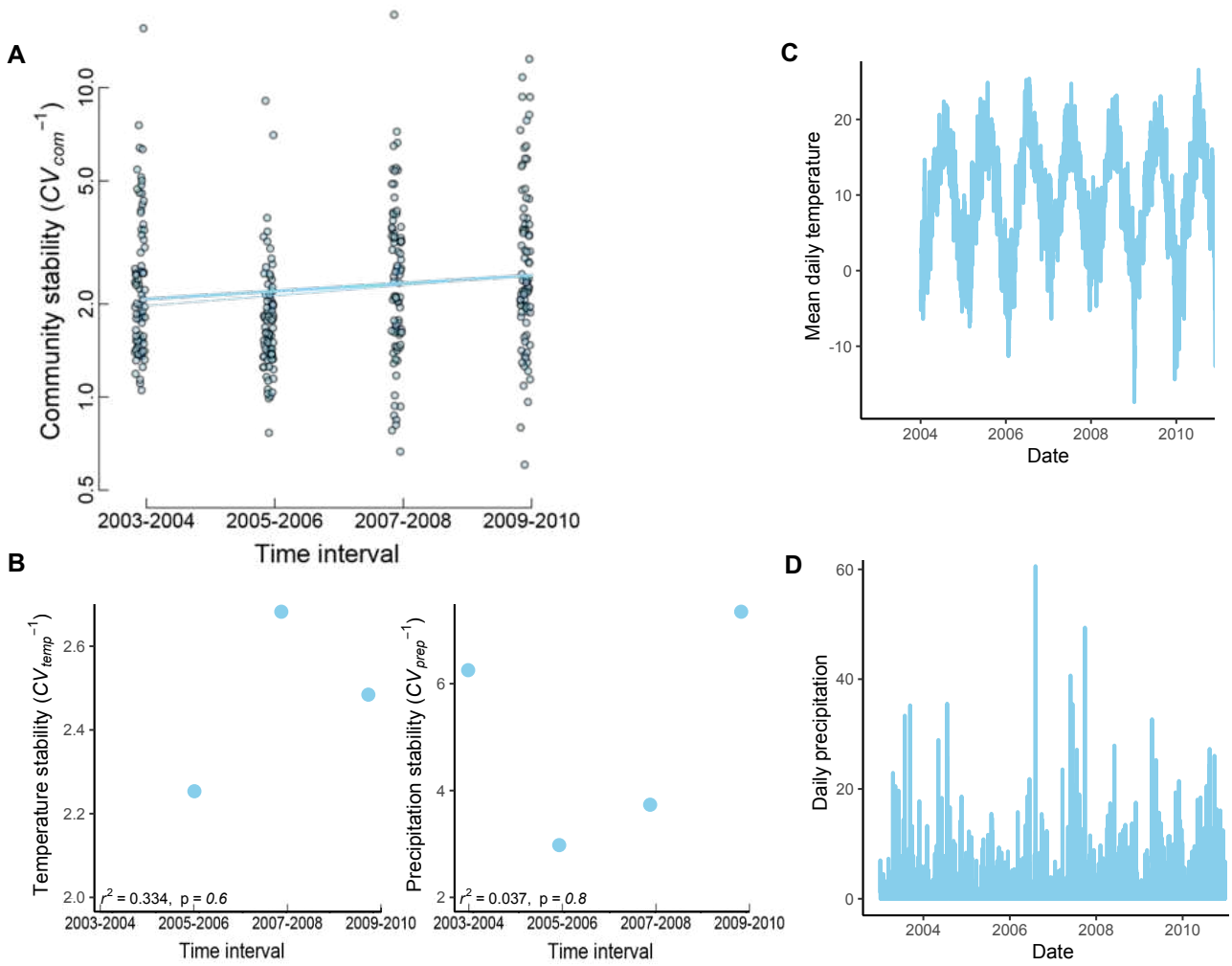


**Appendix S1: FIG. S1. Stability of community biomass and climate from 2003 to 2010.** (**A**) Combined intra- and inter-annual stability of experimental communities over the first 8 years in a grassland biodiversity experiment (Jena Experiment; species richness levels: 1, 2, 4, 8, 16, 60). The 8-year period was partitioned into four 2-year periods and within each stability was calculated for spring and summer harvests in year n and spring harvest in year n+1, corresponding to the same sequence of three harvests used in subsequent tests communities collected from the Jena Experiment in 2010 (selected communities) or re-established from seeds of the original supplier (naïve communities). Thick regression line includes three outliers outside the top margin of the plot ($P = 0.037$), thin line excludes these outliers ($P = 0.0018$). Changes in community biomass stability over time were also significantly correlated with precipitation stability ($P < 0.001$ when "precipitation stability" is fitted in the model instead of the term "time"). **(B)** Stability (inverse of the CV) over time for mean temperatures and precipitation in spring (March-May) and summer (June-August), times that correspond to the growth of biomass. The CV was calculated across three time points (spring year n, summer year n and spring year n+1). Temperature from the year 2003 is missing, which is why the first value appears in 2004. Note that the CV is the inverse of stability, thus lower values mean higher stability. Test statistics are shown in the figure. (**C**) Mean temperatures from 2003 to 2010. (**D**) Total daily precipitation from 2003 to 2010. Temperature and precipitation were measured with a weather station on site (see Appendix S1: Fig. S1C, D).

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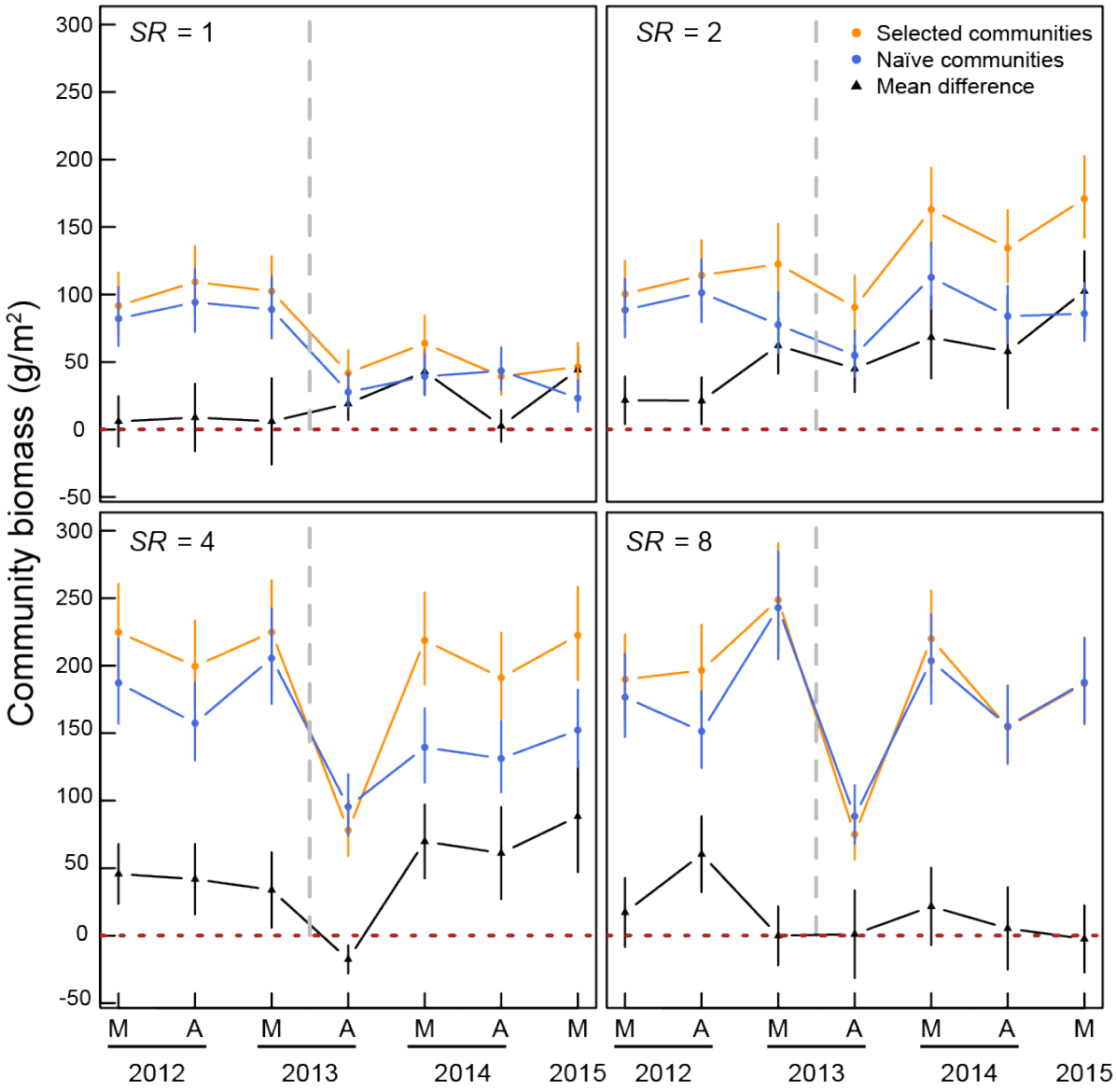
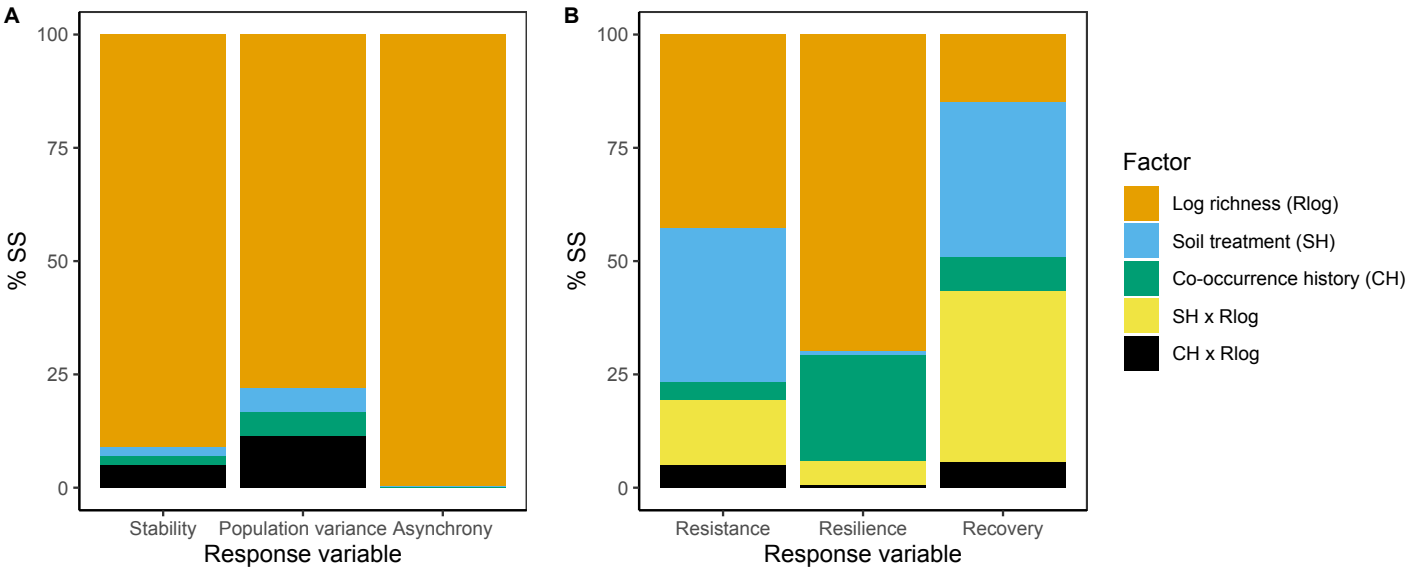
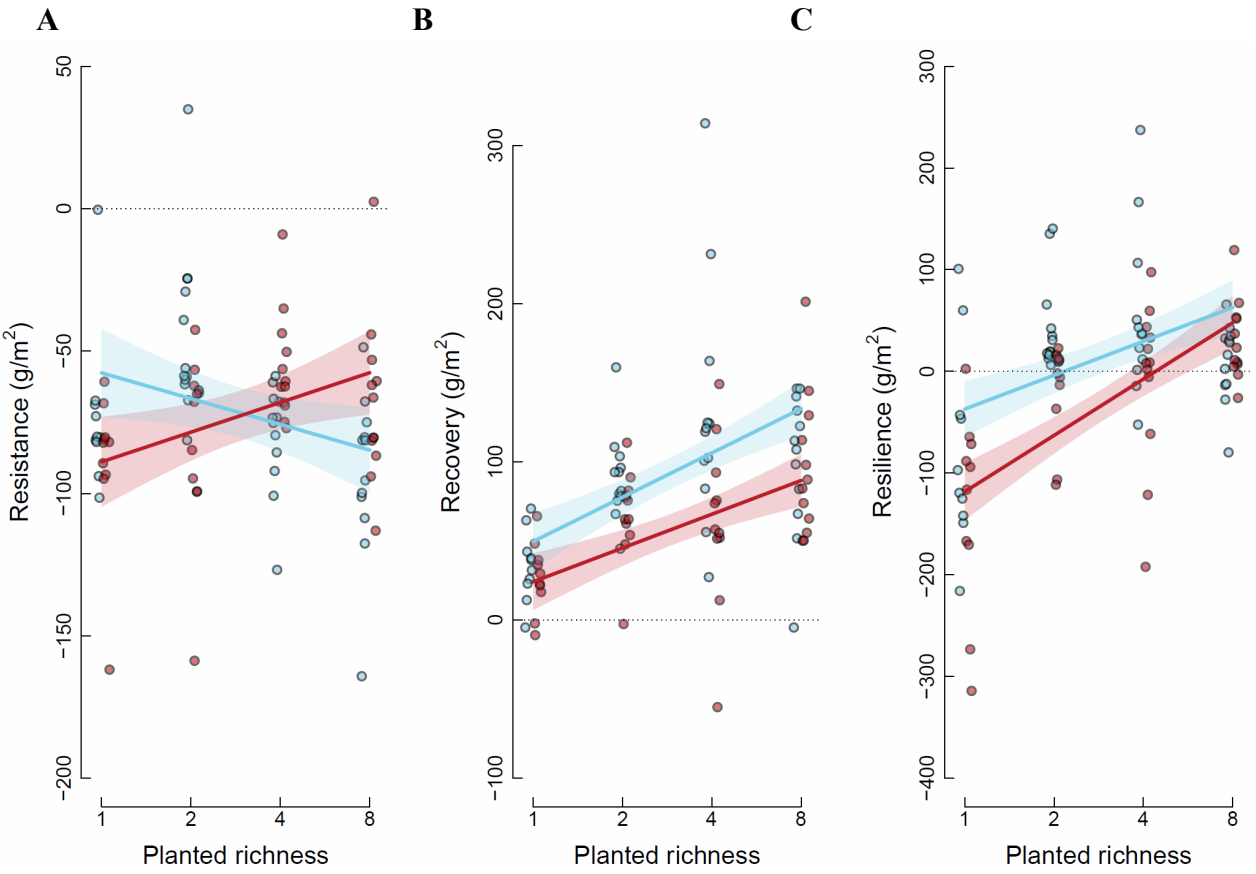


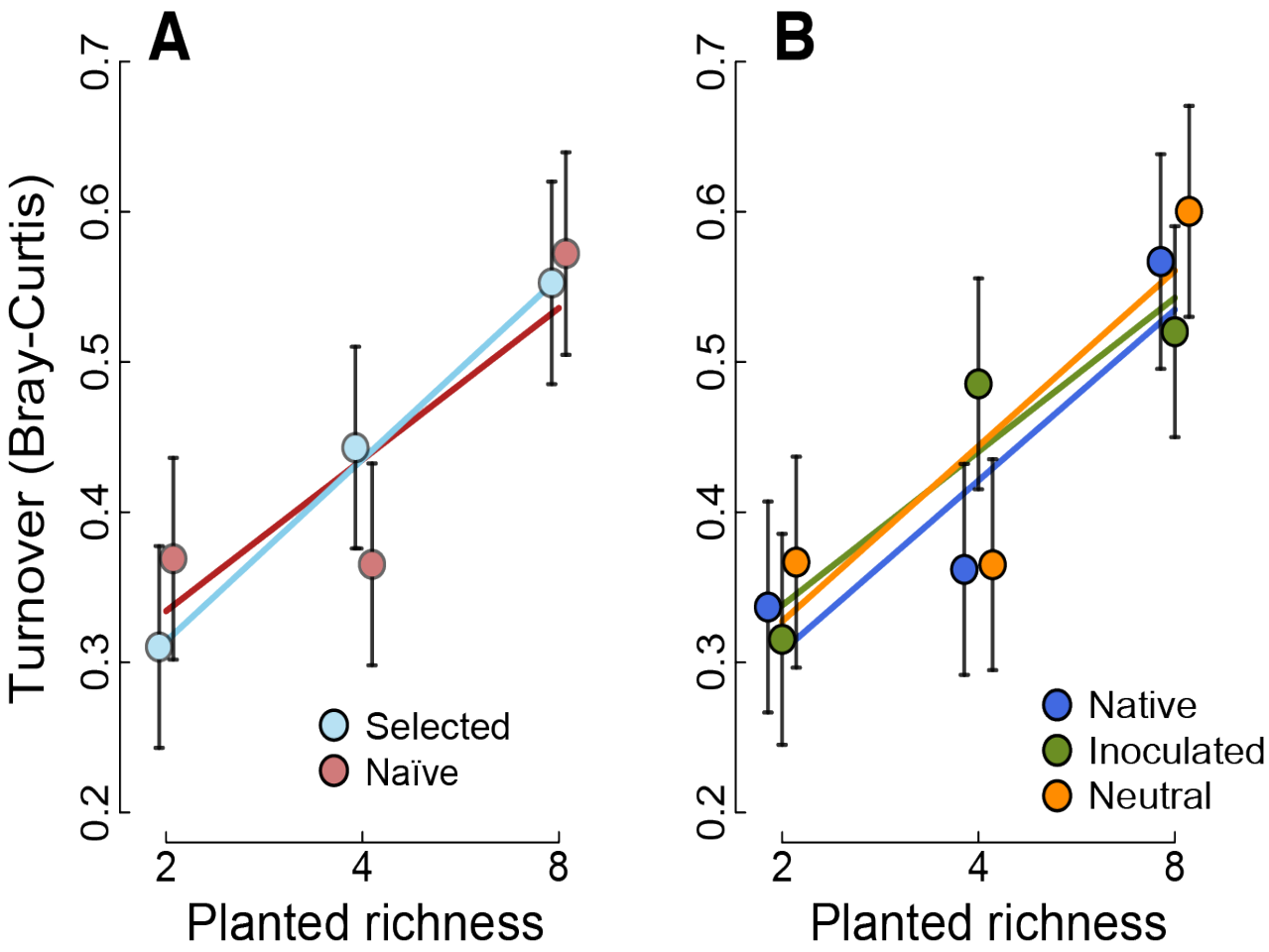

**Appendix S1: FIG. S2. Aboveground community biomass over time at four species richness levels (SR).** Selected and naïve plant communities and their mean difference are plotted with means and standard errors calculated from raw data. The dashed line indicates the flood event. M = May, A= August. For the calculation of resistance, resilience, and recovery, we averaged the community biomass in May 2012, August 2012, and May 2013 to obtain pre-flood biomass. We used the August 2013 biomass as our measure of biomass during the flood (even though we harvested several weeks after the water had receded). For post-flood biomass we averaged community biomasses from May 2014, August 2014, and May 2015.




**Appendix S1: FIG. S3. Effect sizes (% SS) for fixed factors from a linear model. (A)** Asynchrony, population variance and community stability. **(B)** Recovery, resilience, and resistance**.** We used linear models to get % SS as effect sizes to compare relative explanatory power of the different fixed effects tested in the mixed models as done in hierarchical partitioning(Grömping 2006). Note that, due the almost fully orthogonal experimental design, % SS for different fitting sequences and results from linear and mixed models were nearly identical.




**Appendix S1: FIG. S4. Resistance, recovery, and resilience corrected for pre-flood biomass.** **(A)** Biodiversity–resistance relationships, **(B)** biodiversity–recovery relationships and **(C)** biodiversity–resilience relationships for selected (blue) and naïve communities (red). Colored bands indicate standard errors of predictions from mixed models as presented in Table S1. In contrast to Fig. 4 in the main text here the raw data were not only corrected for variation within diversity levels between plots and quadrats but also for variation in pre-flood biomass. Means across the three soil treatments are shown. The dashed line is drawn at 0 in each graph.




**Appendix S1: FIG. S5. The biodiversity–turnover relationship. (A)** Selected (blue) and naïve communities (red). **(B)** Home soil (blue), sterilized soil with native inoculum ("inoculated", green) and sterilized soil with neutral inoculum ("neutral", orange). Species compositional turnover was calculated between three pre- and three post-flood harvests. The species richness effect was significant but none of the other effects and none of the interactions were significant (see Appendix S1: Table S3). Shown are predicted means and standard errors.

**Appendix S1: TABLE S1.** Mixed-model ANOVA results for pre-flood biomass-corrected resistance, recovery, and resilience of community biomass. The effects of species richness (log scale), soil treatments and co-occurrence history on responses of community biomass to flooding were analyzed. In contrast to Table 2 (and the corresponding Fig. 4) in the main text, here the average of the three harvests before the flood (pre-flood productivity) was included as a covariate to account for the dependence of resistance, recovery, and resilience measures on the initial productivity. Bold italic text highlights significant effects.

| | | **Resistance** | | | **Recovery** | | | **Resilience** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fixed terms | $DF_{num}$ | $DF_{den}$ | *F* | *P* | $DF_{den}$ | *F* | *P* | $DF_{den}$ | *F* | *P* |
| Pre-flood productivity | 1 | ***239.0*** | ***271.60*** | ***<0.001*** | ***199.7*** | ***17.05*** | ***<0.001*** | ***223.8*** | ***47.75*** | ***<0.001*** |
| Log richness ($R_{log}$) | 1 | 48.4 | 0.02 | 0.886 | ***49.6*** | ***9.53*** | ***0.003*** | ***49.2*** | ***11.50*** | ***0.001*** |
| Soil treatment (SH) | 2 | 96.2 | 0.41 | 0.668 | 95.2 | 0.13 | 0.877 | 96.4 | 1.50 | 0.229 |
| Co-occurrence history (CH) | 1 | 140.3 | 0.03 | 0.860 | ***140.0*** | ***11.65*** | ***<0.001*** | ***140.7*** | ***10.95*** | ***0.001*** |
| SH x $R_{log}$ | 2 | 90.3 | 1.23 | 0.296 | 89.5 | 2.39 | 0.097 | ***90.5*** | ***3.75*** | ***0.027*** |
| CH x $R_{log}$ | 1 | ***133.9*** | ***8.77*** | ***0.004*** | 134.4 | 0.48 | 0.491 | 134.6 | 2.84 | 0.094 |
| Random terms | *N* | *Var.* | *SE* | | *Var.* | *SE* | | *Var.* | *SE* | |
| Plot | 46 | 2124 | 643 | | 1887 | 717 | | 5971 | 1920 | |
| Plot x SH | 137 | 669 | 429 | | 112 | 756 | | 1265 | 1521 | |
| Residual | 274 | 3534 | 432 | | 7583 | 925 | | 14035 | 1711 | |

*Note*: $DF_{num}$ = numerator degrees of freedom, $DF_{den}$ = denominator degrees of freedom, *F* = variance ratio, *P* = probability of type-I error.

**Appendix S1: TABLE S2.** Mixed-model ANOVA results for log-transformed community stability for the three harvests before the flood event in late spring of June 2013 (pre-flood stability) and the three harvests after recovery from the flood event (post-flood stability). The effects of species richness (log scale), soil treatments, and co-occurrence history on the pre- and post-flood stability of community biomass were analyzed. Bold italic text highlights significant effects.

| | | **Pre-flood stability** | | | **Post-flood stability** | | |
|---|---|---|---|---|---|---|---|
| Fixed terms | $DF_{num}$ | $DF_{den}$ | *F* | *P* | $DF_{den}$ | *F* | *P* |
| Log richness ($R_{log}$) | 1 | 44.1 | 1.67 | 0.203 | ***43.9*** | ***13.89*** | ***<0.001*** |
| Soil treatment (SH) | 2 | 86.2 | 1.04 | 0.356 | 86.3 | 0.99 | 0.377 |
| Co-occurrence history (CH) | 1 | 133.1 | 1.50 | 0.222 | ***133.6*** | ***5.03*** | ***0.027*** |
| SH x $R_{log}$ | 2 | 87.9 | 2.26 | 0.110 | 87.1 | 0.28 | 0.754 |
| CH x $R_{log}$ | 1 | 134.5 | 2.86 | 0.093 | 134.1 | 0.10 | 0.749 |
| Random terms | *N* | *Var.* | *SE* | | *Var.* | *SE* | |
| Plot | 36 | 0.273 | 0.069 | | 0.092 | 0.032 | |
| Plot x SH | 107 | 0.008 | 0.027 | | -0.013 | 0.030 | |
| Residual | 214 | 0.267 | 0.033 | | 0.321 | 0.039 | |

*Note*: $DF_{num}$ = numerator degrees of freedom, $DF_{den}$ = denominator degrees of freedom, *F* = variance ratio, *P* = probability of type-I error.

**Appendix S1: TABLE S3.** Mixed-model ANOVA results for Bray-Curtis compositional turnover between three pre- and three post-flood harvests. The effects of species richness (log scale), soil treatments, and co-occurrence history on the compositional turnover were analyzed. Bold italic text highlights significant effects.

| | | **Turnover** | | |
|---|---|---|---|---|
| Fixed terms | $DF_{num}$ | $DF_{den}$ | $F$ | $P$ |
| Log richness ($R_{log}$) | 1 | ***34.0*** | ***6.25*** | ***0.017*** |
| Soil treatment (SH) | 2 | 67.1 | 0.30 | 0.744 |
| Co-occurrence history (CH) | 1 | 105.0 | 0.00 | 1.000 |
| SH x $R_{log}$ | 2 | 67.1 | 0.08 | 0.927 |
| CH x $R_{log}$ | 1 | 105.0 | 0.40 | 0.527 |
| Random terms | $N$ | *Var.* $10^{-3}$ | *SE* $10^{-3}$ | |
| Plot | 36 | 41.29 | 11.55 | |
| Plot x SH | 107 | 0.00 | 4.00 | |
| Residual | 214 | 35.95 | 4.96 | |

**Appendix S1: TABLE S4. Analysis of soil-history treatments at the end of the experiment in October 2015.** Means and standard errors (SEMs) are given together with the *P*-values testing the significance of treatment effects in analyses of variance. SEMs were calculated with the raw data.

| | **Native soil** | | **Sterilized soil with native inoculum** | | **Sterilized soil with neutral inoculum** | | |
|---|---|---|---|---|---|---|---|
| Soil characteristics | Mean | SEM | Mean | SEM | Mean | SEM | Significance |
| Nitrate (ppm) | 7 | 0.26 | 5.7 | 0.26 | 5.5 | 0.25 | < 0.001 |
| Phosphorous (ppm) | 23.5 | 1.5 | 31.1 | 1.8 | 31 | 1.9 | < 0.001 |
| Microbial carbon | 626.5 | 16.1 | 451.8 | 14.2 | 442.3 | 14.6 | < 0.001 |
| Microbial nitrogen | 150.7 | 3.5 | 112.2 | 3.1 | 106.1 | 3.3 | < 0.001 |
| Bacterial richness (# 16S-OTUs) | 5230.4 | 71.1 | 4919.9 | 82 | 4822.5 | 92.1 | < 0.001 |
| Bacterial evenness | 0.889 | 8E-04 | 0.875 | 0.0007 | 0.864 | 0.00082 | < 0.001 |
| Fungal richness (# ITS-OTUs) | 774.8 | 17.9 | 765.7 | 17.6 | 765.9 | 19 | 0.1 |
| Fungal evenness | 0.879 | 0.002 | 0.885 | 0.0013 | 0.888 | 0.00148 | < 0.001 |

**Appendix S1: TABLE S5. Species list.** In the 47 experimental communities, a total of 49 species were grown in different community diversities and compositions. The eleven species occurring in monoculture are highlighted in bold. For species authorities and definition of functional groups see (Roscher et al. 2004). Biomass values are taken from small 3.5 x 3.5 m monoculture plots and represent yearly aboveground averages from 2003–2006 (Marquard et al. 2013).

| Species | Functional group | Life cycle | Self-incompatible (yes/no) | Biomass ($g/m^2$) |
|---|---|---|---|---|
| *Achillea millefolium* | herb | perennial | yes | 338.0 |
| *Ajuga reptans* | herb | perennial | no | 10.1 |
| *Alopecurus pratensis* | grass | perennial | no | 433.9 |
| *Anthoxanthum odoratum* | grass | perennial | no | 259.6 |
| *Arrhenatherum elatius* | grass | perennial | yes | 616.4 |
| *Avenula pubescens* | grass | perennial | yes | 422.6 |
| *Bromus erectus* | grass | perennial | yes | 675.5 |
| *Bromus hordeaceus* | grass | annual–biennial | no (mostly selfing) | 251.6 |
| ***Crepis biennis*** | herb | perennial | no | 326.4 |
| *Cynosurus cristatus* | grass | perennial | yes | 78.2 |
| *Dactylis glomerata* | grass | perennial | yes | 462.5 |
| *Daucus carota* | herb | biennial | yes | 376.9 |
| *Festuca pratensis* | grass | perennial | yes | 329.9 |
| ***Festuca rubra*** | grass | perennial | no | 334.7 |
| ***Galium mollugo*** | herb | annual | no | 438.1 |
| ***Geranium pratense*** | herb | perennial | no | 262.1 |
| *Glechoma hederacea* | herb | perennial | no | 92.8 |
| *Heracleum sphondylium* | herb | biennial–perennial | no | 180.0 |
| *Holcus lanatus* | grass | perennial | mostly yes | 500.7 |
| *Knautia arvensis* | herb | perennial | no | 644.4 |
| ***Lathyrus pratensis*** | legume | perennial | no | 357.8 |
| *Leontodon autumnalis* | herb | perennial | yes | 290.8 |
| *Leontodon hispidus* | herb | perennial | no | 331.8 |
| *Leucanthemum vulgare* | herb | perennial | yes | 445.6 |
| *Lotus corniculatus* | legume | perennial | mostly yes | 388.0 |
| *Luzula campestris* | grass | perennial | mostly yes | 0.1 |
| *Medicago lupulina* | legume | annual–perennial | no | 52.4 |
| *Medicago x varia* | legume | perennial | no | 815.9 |
| ***Onobrychis viciifolia*** | legume | perennial | no | 1290.5 |
| *Phleum pratense* | grass | perennial | mostly yes | 417.8 |
| ***Plantago lanceolata*** | herb | perennial | yes | 224.6 |
| *Plantago media* | herb | perennial | no | 420.8 |
| ***Poa pratensis*** | grass | perennial | no | 235.0 |
| *Poa trivialis* | grass | perennial | no | 164.7 |
| *Primula veris* | herb | perennial | yes | 168.1 |

| | | | | |
|---|---|---|---|---|
| ***Prunella vulgaris*** | herb | perennial | no | 222.3 |
| *Ranunculus acris* | herb | perennial | yes | 242.7 |
| *Ranunculus repens* | herb | perennial | yes | 132.4 |
| *Sanguisorba officinalis* | herb | perennial | no | 414.7 |
| *Taraxacum officinale* | herb | perennial | yes | 286.2 |
| *Trifolium campestre* | legume | annual | no | 8.9 |
| *Trifolium dubium* | legume | annual | yes? | 2.8 |
| *Trisetum flavescens* | grass | perennial | yes? | 422.6 |
| *Trifolium fragiferum* | legume | perennial | mostly yes | 143.1 |
| *Trifolium hybridum* | legume | perennial | mostly yes | 227.1 |
| *Trifolium pratense* | legume | perennial | yes | 353.1 |
| ***Trifolium repens*** | legume | perennial | yes | 361.4 |
| ***Veronica chamaedrys*** | herb | perennial | yes | 220.2 |
| *Vicia cracca* | legume | perennial | no | 93.2 |

**Appendix S1: TABLE S6. Overview of seeds collected in the Jena plots.** For those species that did not produce enough seeds in the experimental garden in Zurich, some additional seeds were collected directly in the Jena experimental plots. Shown are percentages of total seed weight with an origin of the Jena plots for each species in each experimental community.

| Plot | SR | Species | %seeds collected in Jena | Plot | SR | Species | %seeds collected in Jena | Plot | SR | Species | %seeds collected in Jena |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **B1A01** | **16** | Pla lan | 21.4 | **B2A01** | **4** | Ant odo | 0.0 | **B3A04** | **8** | Alo pra | 0.0 |
| | | Lat pra | 0.0 | | | Pru vul | 0.0 | | | Cyn cri | 0.0 |
| | | Poa pra | 0.0 | | | Kna arv | 0.0 | | | Fes rub | 0.0 |
| | | Ger pra | 1.1 | | | Tri pra | 0.0 | | | Poa tri | 0.0 |
| **B1A02** | **8** | Alo pra | 29.7 | **B2A02** | **2** | Fes rub | 0.0 | | | Arr ela | 0.0 |
| | | Bro ere | 0.0 | | | Tri fla | 0.0 | | | Dac glo | 0.0 |
| | | Car pra | 0.0 | **B2A03** | **60** | Fes pra | 100.0 | | | Hol lan | 0.0 |
| | | Her sph | 0.0 | | | Fes rub | 0.0 | | | Tri fla | 0.0 |
| | | Fes rub | 0.0 | | | Pru vul | 0.0 | **B3A05** | **8** | Ant odo | 0.0 |
| | | Phl pra | 0.0 | | | Ver cha | 100.0 | | | Bro ere | 0.0 |
| | | Ran acr | 63.0 | | | Poa pra | 0.0 | | | Poa tri | 20.5 |
| | | San off | 0.0 | | | Pla lan | 100.0 | | | Ant syl | 100.0 |
| **B1A03** | **8** | Cyn cri | 0.0 | **B2A04** | **1** | Ger pra | 0.0 | | | Leu vul | 0.0 |
| | | Phl pra | 0.0 | **B2A05** | **1** | Fes pra | 0.0 | | | Lot cor | 5.0 |
| | | Gle hed | 0.0 | **B2A06** | **4** | Pla lan | 10.3 | | | Ono vic | 99.9 |
| | | Pri ver | 0.0 | | | Tar off | 0.0 | | | Tri hyb | 0.0 |
| | | Tri fla | 0.0 | | | Lat pra | 73.7 | **B3A06** | **1** | Fes rub | 53.0 |
| | | Ver cha | 0.0 | | | Med lup | 0.0 | **B3A07** | **8** | Bro hor | 0.0 |
| | | Lot cor | 0.0 | **B2A08** | **2** | Ran acr | 20.4 | | | Hol lan | 0.0 |
| few seed | | Med lup | 0.0 | | | Tri cam | 0.0 | | | Pri ver | 0.0 |
| **B1A04** | **4** | Fes pra | 0.0 | **B2A09** | **4** | Aju rep | 0.0 | | | Ran rep | 100.0 |
| | | Pla lan | 33.0 | | | Pla lan | 4.6 | | | Her sph | 0.0 |
| | | Cam pat | 0.0 | | | Pri ver | 0.0 | | | Leu vul | 0.0 |
| | | Ono vic | 0.0 | | | Pru vul | 3.6 | | | Med lup | 0.0 |
| **B1A05** | **2** | Med lup | 0.0 | **B2A12** | **8** | Ant syl | 0.0 | | | Ono vic | 82.7 |
| | | Ono vic | 0.0 | | | Ger pra | 0.0 | **B3A08** | **2** | Dac glo | 0.0 |
| **B1A07** | **2** | Ran acr | 17.2 | | | Kna arv | 52.6 | | | Fes pra | 0.0 |
| | | San off | 0.0 | | | Ran acr | 4.3 | **B3A09** | **16** | Fes pra | 94.0 |
| **B1A11** | **16** | Ger pra | 0.0 | | | Gal mol | 0.0 | | | Fes rub | 0.0 |
| | | Cre bie | 10.1 | | | Her sph | 0.0 | | | Poa pra | 0.0 |
| | | Gal mol | 0.0 | | | Leu vul | 0.0 | **B3A11** | **4** | Bro ere | 0.0 |
| **B1A12** | **8** | Lat pra | 0.0 | | | San off | 0.0 | | | Poa tri | 0.0 |
| | | Med var | 0.0 | **B2A13** | **1** | Pla lan | 1.2 | | | Pla lan | 6.7 |
| few seed | | Tri cam | 0.0 | **B2A14** | **8** | Luz cam | 0.0 | | | Pru vul | 2.1 |
| | | Tri hyb | 0.0 | | | Phl pra | 0.0 | **B3A12** | **1** | Lat pra | 30.1 |
| | | Med lup | 0.0 | | | Leo his | 0.0 | **B3A13** | **4** | Alo pra | 0.0 |
| | | Ono vic | 81.2 | | | Ver cha | 0.0 | | | Bro ere | 96.3 |
| | | Tri dub | 0.0 | | | Kna arv | 79.9 | | | Ant odo | 0.0 |
| | | Tri pra | 0.0 | | | San off | 0.0 | | | Poa tri | 0.0 |
| **B1A13** | **4** | Lot cor | 0.0 | | | Tri dub | 0.0 | **B3A17** | **1** | Ver cha | 30.0 |
| | | Med var | 0.0 | | | Tri hyb | 5.5 | **B3A19** | **2** | Tri fla | 0.0 |
| | | Ono vic | 0.0 | **B2A15** | **1** | Ono vic | 48.1 | | | Tar off | 0.0 |
| | | Med lup | 0.0 | **B2A16** | **4** | Leo aut | 0.0 | **B3A21** | **2** | Lot cor | 0.5 |

| | | | |
|---|---|---|---|
| **B1A14** | **8** | Luz cam | 0.0 |
| | | Tri fla | 0.0 |
| | | Leo his | 0.0 |
| | | Pla lan | 28.4 |
| | | Ant syl | 0.0 |
| | | Dau car | 0.0 |
| | | Tri cam | 8.4 |
| | | Tri fra | 0.0 |
| **B1A15** | **1** | Cre bie | 0.0 |
| **B1A16** | **2** | Poa pra | 0.0 |
| | | Pla lan | 6.0 |
| **B1A17** | **2** | Alo pra | 46.6 |
| | | Dau car | 0.0 |
| **B1A18** | **1** | Pru vul | 2.4 |
| **B1A19** | **4** | Arr ela | 31.8 |
| | | Luz cam | 0.0 |
| | | Pru vul | 0.0 |
| | | Cam pat | 0.0 |
| **B1A21** | **4** | Fes pra | 0.0 |
| | | Luz cam | 0.0 |
| | | Ach mil | 0.0 |
| | | Cre bie | 0.0 |
| **B1A22** | **60** | Fes pra | 0.0 |
| | | Fes rub | 0.0 |
| | | Pru vul | 0.0 |
| | | Ver cha | 0.0 |
| | | Ger pra | 0.0 |
| | | Poa pra | 0.0 |
| | | Pla lan | 8.1 |
| | | Pla med | 9.6 |
| | | Kna arv | 80.4 |
| | | Vic cra | 0.0 |
| **B2A17** | **8** | Gle hed | 0.0 |
| | | Pla med | 25.2 |
| | | Leo aut | 0.0 |
| | | Tar off | 0.0 |
| | | Lat pra | 0.0 |
| | | Vic cra | 47.9 |
| | | Tri cam | 0.0 |
| | | Tri fra | 0.0 |
| **B2A18** | **16** | Poa pra | 0.0 |
| | | Ger pra | 0.0 |
| | | Tri rep | 18.5 |
| **B2A19** | **2** | Pla med | 23.9 |
| | | Tar off | 0.0 |
| **B2A20** | **2** | Pla lan | 8.0 |
| | | Tri dub | 0.0 |
| **B2A21** | **8** | Leo his | 23.0 |
| | | Pla med | 49.7 |
| | | Cre bie | 0.0 |
| | | Gal mol | 0.0 |
| | | Lot cor | 69.9 |
| | | Med lup | 0.0 |
| | | San off | 65.1 |
| | | Ono vic | 92.1 |
| **B3A01** | **1** | Gal mol | 92.5 |
| **B3A02** | **2** | Fes pra | 0.0 |
| | | Car car | 0.0 |
| **B3A03** | **4** | Phl pra | 0.0 |
| | | Pla med | 55.3 |
| | | Tri hyb | 0.0 |
| | | Vic cra | 25.1 |
| | | Tri pra | 0.0 |
| **B3A22** | **16** | Fes rub | 0.0 |
| | | Ver cha | 0.0 |
| | | Cre bie | 0.7 |
| | | Ger pra | 41.6 |
| | | Gal mol | 99.7 |
| | | Pla lan | 100.0 |
| | | Ono vic | 0.0 |
| **B4A06** | **8** | Pru vul | 0.0 |
| | | Ver cha | 0.0 |
| **B4A08** | **8** | Ant odo | 0.0 |
| | | Bro hor | 0.0 |
| | | Ave pub | 0.0 |
| | | Fes rub | 0.0 |
| | | Aju rep | 0.0 |
| | | Tar off | 0.0 |
| | | Pla lan | 22.1 |
| | | Ver cha | 100.0 |
| **B4A09** | **1** | Tri rep | 0.0 |
| **B4A12** | **1** | Poa pra | 45.1 |
| **B4A18** | **16** | Ver cha | 78.1 |
| | | Cre bie | 0.0 |
| | | Lat pra | 83.8 |
| | | Ono vic | 97.5 |
| **B4A22** | **4** | Cam pat | 0.0 |
| | | Ger pra | 0.0 |
| | | Car pra | 0.0 |
| | | Kna arv | 0.0 |

## Appendix S1: LITERATURE CITED

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Roscher, C., J. Schumacher, J. Baade, W. Wilcke, G. Gleixner, W. W. Weisser, B. Schmid, and E.-D. Schulze. 2004. The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. Basic and Applied Ecology 5:107–121.